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PHYSIOLOGICAL ONTOGENY

I. THE PRESENT STATUS OF THE PROBLEM

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INTRODUCTION

EVERY pattern in nature has its own intrinsic set of properties, and the correlation of the two—patterns and properties—is an interest germane to science. It is of particular consequence when it involves a progressive sequence of correlations in a system characterized by unstable dynamic equilibria. In biology this would be the case for the series of organic changes in the life span of an individual being. It is the purpose of these investigations to discover relationships between the structure and the behavior of an organism as functions of age. The subject may be divided into two parts—namely, a study of (1) the modifications of form, and by this is meant the chemical constitution as well as the gross and microscopic structure, and (2) the changes in function. Thus two age old problems in consequence are involved: (1) the relationship of structure and behavior and (2) the problem of aging.

It is suggested that life is an irreversible process and that every organism of whatever species, as a whole or in any of its parts, being what it is and having the properties which it seems to have, will tend to exhibit similar fundamental manifestations and dispositions in the processes of growth, differentiation, and senescence. In other words it is assumed that within limits there is an essential order in all kinds of evolution.

In a world of great complexity, the attention of man is turned with relief to the more determinate limits of life, creation and death. The very definiteness of such points heightens the sense of reality. Death, in particular, is characterized by a finality which seems decisive. But death is only the end point in a long chain of events, and biologically it may be best understood in terms of the antecedent physico-chemical processes.

Although life, as a concept, has never been given a definition satisfactory to all biologists, there has been considerable unanimity about the ultimately significant characteristics or properties of living matter, common to all its forms. These prop-

erties have not, however, been systematically measured in terms of age, although it is obvious that time is a dimension which should not be neglected in any physiological outlook.

For biological science we believe there is no greater task confronting its disciples than the formulation of a concept that will adequately describe the progress of life itself. Since the earliest times it has been recognized that there is an order in nature and that this order is not a static condition but a dynamic "becoming" in which similar events seem to recur in a more or less periodic fashion. The life of an individual may be considered as a definite cycle with a beginning and an ending. If special attention is given to the functional aspects, the study may properly be called physiological ontogeny. Later, physiology may be correlated with morphology. One may deal with the whole organism or with a particular system.

Attempts have been made in the past to ascribe death to the senescence of some one organ. Such a point of view, however, does not change the general problem, even though it might lead one to concentrate attention upon a particular part. It is safe to suppose that if this special part could be prevented from undergoing morbid change, death would occur as a result of aging in some other organ, for the viability of the total organism depends upon the coördinated activity of its integral parts. It may be assumed, therefore, for theoretical purposes that natural death coincides with the simultaneous cessation of activity in all the cells of the body, even though it is recognized that in any one case this probably never occurs.

Keith Lucas, referring to physiological evolution, a subject that he considered of the first magnitude, emphasized the importance of investigating differences in functional capability rather than normal behavior, or in other words, the behavioristic differences that could be brought out under special experimental conditions. Lucas called it "the primary problem of comparative physiology—a problem whose investigation is wholly necessary for the understanding of the evolutionary process. It may be stated in general terms as the question to what extent and along what lines the functional capabilities of animal cells have been changed in the course of evolution."

Before discussing the methods of investigation and the results of our preliminary studies in physiological ontogeny it would be well to review the available relevant facts and the various hypotheses that have been advanced to describe them.

BIOLOGY

The chief facts pertaining to the phenomenon of aging, of which there are a great variety, have been derived from investigations upon the lower forms of life. It is not a simple matter to estimate them. A review of the literature discloses many apparently irreconcilable contradictions. The difficulty is due to the customary practice of each observer of focussing his attention upon a single part only of the multiformity of organic change, and even in some instances of proposing the specially selected factor as the "cause" of senescence. Few of the observations may, moreover, be correlated one with another, since they deal with different species or with the same species over different periods of the life span. To arrive at a comprehensive view of the developmental process a more systematic treatment involving the simultaneous analysis of numerous functions over the same developmental cycle is required.

It is now generally agreed that unicellu-

lar organisms and perhaps any tissues in the body of the metazoan when freed from the organizing or integrating forces of their own milieux are potentially immortal. Under experimental conditions when the environment, as for instance culture media, whether of tissue cells or of bacteria, is regularly refreshed, growth continues indefinitely and at a continuous rate theoretically, that is to say by geometrical progression. The experiments of Woodruff with paramecia, Carrel with fibroblasts, Leo Loeb with transplanted tumors, and Felton with bacterial microorganisms are perhaps the most convincing of such researches. In a state of nature, however, eventually the increase in numbers causes congestion, and in consequence competition for available nutriment. Regularly then as the food supply becomes inadequate some of the less adapted or adaptable individuals die without division and the growth rate of the colony declines and eventually comes to a dead level. In both instances, either under experimental or under natural conditions, the individuals of the colony show evidences of growth, differentiation, and senescence, followed by division and rejuvenescence, but in the former state where there is no limit to growth the two processes of differentiation and dedifferentiation may balance each other so that with time there is no predominance of differentiation, whereas in nature it is possible that a "slow progressive senescence may occur extending through many generations" (Child). With a limited quantity of food, however, such as in an untransplanted bacterial culture all the living cells eventually die. A condition such as this is somewhat similar to the state of affairs in a single multicellular organism which may be viewed as a colony of cells the environment (that is to say internal environment) of which is continually undergoing alteration and becoming less fit. The former (colonies of bacteria) may be used as examples of phylogenetic or racial, the latter (metazoa) of ontogenetic or individual senescence and death. In both cases there is that reciprocal dependence. The active constituents progressively modify their immediate surroundings, and the latter in turn modify the velocity and nature of the vital functions. In the case of racial growth the degradation of activity may be remedied by experimental revivification of the environment. In the metazoa the existence and nature of their organization prevent this. It seems to depend upon the dominance of what might be termed spheres of control, so that except under abnormal or artificial conditions (as for instance in the case of neoplasms and tissue cultures) the cells do not and cannot escape from their own progressively deteriorating environment.

The distinction between the protozoa and the metazoa on the basis of immortality is, however, somewhat misleading, because even under natural conditions the sex cells of the metazoa are potentially immortal. From this point of view the soma may be regarded as a mere appendage—highly differentiated, but affording temporary lodging only for the immortal germ plasm, and destined to be periodically destroyed and renewed in the interests of the race.

Our own interests are concerned not with racial evolution but with the analogous phenomenon, individual evolution. A unicellular organism in its interdivisional period, of course, might be suitably included for study. Each individual protozoon grows, ages, and differentiates, and then either dies or rejuvenates by division; for senescence, but not death, is a phenomenon characteristic of all living matter. It has been observed that with

the growth of a protozoon there is an agglutination of solid material, a formation of metaplastic elements, together with a decrease of surface energy and of osmotic pressure, but as there is no available systematic quantitative treatment of such phenomena during the interdivisional period we may without further delay turn to data from metazoan investigations.

Changes with time may be conveniently divided into those of (1) matter and (2) energy. Under the former heading may be included both growth and form. Changes in form may be observed by a study of gross and microscopic structure, and by the method of chemical analysis. The latter, that is to say changes in energy or function, would include modifications occurring in the natural life history of the organism and also the change with age in reactivity, quantitatively or qualitatively considered, when the organism is subjected to environmental stress, infectious organisms, or untoward experimental procedures. Of course such a division into matter and energy, though convenient, falsifies nature by its arbitrariness. We may profitably recall John Hunter's dictum that "structure is only the ultimate expression of function," or Professor William Wheeler's phrase "form is the excretion of function."

Changes in matter

Growth. Since the time of Quetelet, growth or increase in mass, and form or the result of differential growth in various directions, both as functions of time, have been made the object of numerous statistical studies. (The subject has been treated comprehensively in Professor D'Arcy Thompson's admirable book.) The growth process has not been analyzed, however, so that either the quality of the growth may be known or what seem to be different phenomena (for instance "selective absorption," which involves biological concepts, and osmotic effects, which may be described by physicochemical laws) may be separately apprehended. One must, therefore, use the term in a vague sense to connote the resultant of forces, that is to say the increase in total volume or mass under relatively normal conditions.

It seems that in man, as probably in other species, there are three chief "cycles" of growth. Robertson, who has studied this phase of the subject and has recently summarized the data in a comprehensive fashion, differentiates the following three periods of accelerated anabolic activity: (1) the infantile, with its peak during the latter part of fetal and early months of extra-uterine life; (2) the juvenile, comprising the third, fourth, and fifth years of life; and (3) the adolescent, which occurs at puberty.

The weight curve has in consequence not a simple form. Numerous attempts have nevertheless been made to represent volume, weight, and other dimensional values by single even if not simple mathematical equations with time as the variable. It has not been possible to express the entire span by any rational equation, but by choosing certain phases of it, relatively simple expressions have been found which would fit the portion of the curve selected. Loeb, Ostwald, and Robertson were originally interested in this aspect of the subject and developed conceptions based on the view that growth is an autocatalytic reaction. Later Loeb abandoned the idea, but Robertson carried it into greater detail and elaborated a theory which states that growth rate is determined by a "master reaction" of the order of a monomolecular autocatalytic reaction; this, being the slowest of perhaps a long chain of reactions, governs the rate of all other transformations. The most

recently reported measurements of growth, the results of which have been interpreted by this theory, are those of Brody.

All the objections which arise relative to the autocatalytic hypothesis cannot be enumerated at the present time. No distinction in the theory is made between the growth of a colony of unicellular organisms in unchanged culture medium and that of a single individual, both of which give *S*-shaped curves when the total weight is plotted against time. If growth is expressed in terms of percentage increase in mass, however, the important distinction between phylogenetic and ontogenetic growth is made evident. Colony, racial, or phylogenetic growth (as in the case of bacteria and paramecia), after a short latent period in the presence of an experimentally modified environment, proceeds at a constant rate (compound interest law). The individual organism, on the other hand, instead of maintaining a constant growth rate shows from the beginning considerable negative acceleration, a fact to which Minot was the first to call attention.

The principal objection to the autocatalytic growth law, however, is that it disregards chemical differentiation. It commences by erecting the concept of a "master-reaction," monomolecular in nature, which determines the velocity of organic growth. Since it is obviously impossible to measure the velocity of a reaction, the components and products of which are unknown, the total body weight is taken to represent the result of all the reactions involved, and in this manner the velocity of the theoretical master-reaction. This step depends for its validity upon the assumption that there is a constant direct proportionality between the two, that is to say between the total body weight and the mass of the product; an assumption that is obviously unwarranted.

In view of the facts relative to chemical differentiation it is difficult to see how any equation to describe such an infinitely complicated process as growth could have more than statistical significance. In fact dry weight would seem a better criterion of growth than wet weight. For the water in the body may be considered as essentially passive, and the very marked changes with age in its concentration are obedient to significant redistributions and spatial changes amongst the chemical constituents of the protoplasm.

Form. Gross structures. Into a description of the development of specialized parts and of organs we need not enter. This subject has been exhaustively treated in embryological textbooks. The chief gross structural developments as far as the heart—an organ in which we have been especially interested—is concerned are: (1) the separation of auricles and ventricles with the development of valves, (2) the partition into right and left hearts by means of the interventricular and interauricular septa, and (3) the establishment of connections with the central nervous system together with the development of nodal points and a conducting mechanism for the transmission of excitatory impulses. It is commonly assumed that growth and differentiation, both of the whole and of its parts, proceed synchronously. This is unwarranted, for no attempts have been made to measure the velocity of the change in form.

There are facts, however, which indicate that growth and differentiation under certain conditions have a negative correlation. Excessive exposure to light for instance generally retards the growth of plants but may lead to premature differentiation; and conversely growth may proceed at night with the greatest velocity, but the deficiency in illumination may completely inhibit differentiation. Again, the investigations of Gubernatsch,

Cotronei, and Romeis have shown that thyroid gland feeding accelerated differentiation in tadpoles but stunted growth; whereas the effect of feeding thymus gland was the reverse. Morse showed that the action of thyroid gland could be duplicated with iodized amino-acids.

Microscopic structure. Morphologists who have become interested in the problem of aging have for the most part limited themselves to a description of cytological changes such as calcification and pigment formation, characterizing such formation as the cause or the concomitant of old age. But other characterizations of the changes have been proposed. Hodge and Minot called attention to the decrease in the ratio of nucleus to cytoplasm with age. The latter laid the most particular emphasis upon this point and believed it to be the crux of the problem. He did not, however, discover the rate at which this ratio changed with age, nor did he correlate it with other functions to make evident the dependence of one upon the other. His results were later contradicted by the work of Richard Hertwig, who believed on the contrary that the nucleoplasmic ratio increased with age. These histological findings no longer interest us much because of our awareness of the inadequacy of the fixation and staining methods employed to demonstrate the presumed relationship. Recently Le Breton and Schaeffer have used the ratio of purine and non-purine nitrogen as the criterion of the nucleocytoplasmic ratio and, granting the validity of the assumed correlation, have by this method come upon a quantitative measurement of a structural relationship. Their data showed that in chicken embryos the nucleo-cytoplasmic ratio decreased markedly with age.

The accumulation of so-called metaplasmic granules in the cytoplasm has been observed by numerous workers. It is apparent that such elements, hypothetically inert, would mechanically obstruct the passage of molecules and thus decrease the rate of chemical change. Mühlmann, Minot, Hodge, Kassowitz, Conklin, and others have described somewhat similar accretions. Under this head may be classed the lipoid granules in the central nervous system, and the brown pigment in the heart and liver. These and similar histological studies have not been, and cannot hope to be, productive of important results in the search for the chief factors in the mechanism of senescence, unless they are correlated in a more or less systematic fashion with function. In considering changes with development in the cytological aspects of heart muscle the chief points of interest are (1) the changes in composition and in structure of the muscle fiber both in the course of normal growth and in the case of such abnormal growth as is exhibited in hyperplasia and hypertrophy, (2) the history and apparent rôle of elastic tissue, (3) the establishment of nodal centers and (4) the organization of the conducting system. These subjects have been reviewed in a separate chapter in Cowdry's *Special Cytology*.

Chemical constitution. Although a considerable amount of data has been accumulated regarding the chemical constituents of the body of the same and different species at successive periods of the life span, it has yet to be organized into an intelligible form or correlated either with morphological or physiological knowledge. Analyses by Bezold, Liebermann, Weigert, Fehling, Michel, Donaldson, Hatai, and others have taught us that with development there is progressive desiccation of the tissues with a consequent rise in the concentration of nitrogen, fat, and total ash. The ratio of fat to nitrogen also appears to increase with age.

The most comprehensive compilation of data was made by Aron in 1913 and extended in 1921. He included figures for water, nitrogen, fat, and many of the inorganic substances. More recently Moulton has added somewhat similar analyses for swine and cattle. Méndeléef has presented figures which show a gradual rise of the serum pH in guinea pigs during the embryonic and early infantile period, but as the technique, which in this instance is all important, was not described and since some of our own experiments gave opposite results, that is to say a fall in pH with age, one must suspend judgment on this point. Embryonic blood sugars estimated by Aron were variable and difficult to interpret in relation to age. Riddle and Honeywell found no differences in the concentration of blood sugar in pigeons of different ages. (Compare with this the data in human individuals given later.) In most cases the available estimates lack precision and are hardly adequate for further calculations or theoretical treatment.

It would naturally be an error to believe that chemical analyses will yield the basis for constructing the whole picture of physico-chemical differentiation. The properties of protoplasm are dependent as much upon the particular pattern of spatial relationships existing between the elements as upon the nature of these elements. Chemical analysis tends in many instances to destroy this pattern. The analyst loses sight of the very togetherness and wholeness which he would understand, for the inference to be drawn from his procedure is that he is dealing with structureless mixtures of elements.

Changes in function

Numerous biologists, as for instance Kassowitz and Conklin, have developed theories of aging based upon a declining metabolic rate. We have been unable to find, however, that these theories have been supported by any substantial direct experimentation. Benedict has emphasized a decrease in the permeability of the cell membrane with senility in plants, and Osterhout has associated loss of permeability with diminishing conductivity. Child estimated metabolism indirectly by measuring the susceptibility of the organism to cyanides. To prove the relationship of susceptibility and metabolic rate he states that "susceptibility is altered by motor activity, that the temperature coefficient of susceptibility is of the same order of magnitude as that of most chemical reactions and that differences in carbon-dioxide production correspond to differences in susceptibility." From Child's long series of experiments it is evident that susceptibility decreases with age, and from the work of other investigators it appears that the metabolic rate per unit mass declines likewise, but that the former is dependent upon the latter has not been shown. Even if two functions are compared at infrequent intervals and seem to be changing in the same direction, it can hardly be assumed, unless their rates of change are parallel, that they are directly interdependent. Measuring one will not be more than a rough index of the other. It seems that, although the two are in some way related, the evidence is not conclusive that susceptibility to cyanides and anesthetics runs parallel to metabolism. Herlant's experiments, for instance, with the effect of various kinds of poison on eggs suggest by analogy that the times of maximum susceptibility to water soluble and fat soluble toxins respectively are not synchronous in ontogeny. Tests for susceptibility are furthermore not very precise, and the CO_2 output alone, without O_2 determination, is not an entirely satisfactory criterion of

metabolic rate, particularly under abnormal conditions.

Whatever may be the basis of susceptibility, it is a phenomenon of great biological importance, and Child's experiments are of considerable pertinence. Concentrations of the injurious substances were used which kill the organisms within a few hours. There were morphological criteria for the degree of "aliveness" by which at intervals after administration the observer could estimate the effect of the poison. Adaptability or, as Child calls it, acclimation was tested by using concentrations of narcotics which were insufficient to kill within a short period. Organisms for a time seemed to become adapted to such a medium. Death came later, after one or more days. The results of these investigations indicated that the younger tissues were the more susceptible as well as the more adaptable. That is to say, with strong doses they died more rapidly, but with the doses to which acclimation was possible they outlived cells of greater physiological age. Child was not concerned with the rate at which functions, such as stability and mobility, changed with life. Other experiments, conceived as were Child's, have been reported. Tumor cells are generally considered to have the characteristics of young tissue, and their hyper-susceptibility to x-rays and other agents is well known. Warburg, Posener, and Negelein have shown that a similarity exists between the tissues of embryos and of tumor cells in the relation of respiration to glycolysis. The rapidly growing embryos can and do exhibit the phenomenon of aerobic glycolysis to a slight extent, though relying on this function in comparison with rat carcinoma only in the ratio of about 1 to 40. Cramer has shown that susceptibility to x-rays is directly correlated with water content, which in turn is a function of age. Riddle showed that age was the most important factor in determining the death or survival of embryos subjected to abnormal oxygen tensions.

Susceptibility of a different nature, that for instance which is concerned with the reaction to tumor implants, was shown by Murphy to decrease with age in the chicken embryo, or more exactly, resistance to tumor growth seemed to be entirely absent until the 18th day of incubation. At this time small transplants of rat sarcoma would no longer "take," and, even if in full growth at the time, thenceforth became encapsulated and began to show signs of degenerative change.

Brody and his collaborators have used various criteria such as milk secretion and egg production for estimating the rate of aging. It was found here as with growth that an equation of the monomolecular form would describe the relation between age and the empirically ascertained quantities, thus supporting Robertson's theory of the kinetics of senescence. When the growth period is included in the curve describing functional activity, the entire span may be described "by an equation containing two exponential terms which is practically the equation used to represent the course of accumulation and disappearance of a substance as the result of two simultaneous consecutive monomolecular chemical reactions" (Brody). Needham has concerned himself with an analytical study of metabolism. He has reviewed in a comprehensive fashion the metabolism of the developing egg; and further has shown that during the embryological period of the chick there is a succession of energy sources in the order, carbohydrate, protein, and fat.

There is need for a thorough investigation of metabolism in terms of age in some of the lower forms of life for correlation

with successive chemical analyses of the tissues. Life may be viewed in the simplest quantitative terms as exchanges of energy between the organism and its environment, and as transformations, that is to say redistribution, synthesis, storage, and oxidation, of the assimilated energy within the body. Katabolism is the *sine qua non* of life; the heat evolved, as with a coal fire, providing the necessary conditions for its own continued activity. Under basal conditions approximately the minimal heat for the maintenance of life is provided by chemical action. This is the justification for saying that the organism burns in its own flame.

Duration of life

Any discussion of senescence must include a consideration of the factors which affect the velocity of the process. In this connection Loeb and Northrop have made conclusive experiments to show the influence of temperature upon the duration of life of a poikilothermal animal. They found that the life span of sterile flies maintained at different temperatures was considerably shortened by the application of heat; and that the temperature coefficient obtained for these observations was such as one finds for chemical reactions. It seemed, therefore, that life might be viewed as if it were a chemical reaction, which ceased as soon as there was depletion of a particular "life substance" or the accumulation of inhibiting end-products had reached a certain level. The metabolic rate might be accelerated by motor activity as well as by external temperature. Slonaker's few experiments, in which the duration of life in rats forced to exercise in a revolving cage was compared with that of rats kept in stationary cages, showed that under the conditions of the experiment a large amount of exercise was detrimental to longevity.

Other factors having a bearing on this problem have also been studied. Pearl has lately reviewed and summarized the work of eugenicists and statisticians relating the influence of heredity to the length of life. The most reliable and comprehensive data appear to indicate that the dominating factor conditioning the duration of life in a constant environment is an inherited one. Pearl's experiments with *Drosophila* show, furthermore, that the inheritance in question conforms to Mendelian standards. Pearl summarized his general viewpoint by suggesting that heredity probably acts by determining "within fairly narrow limits, the total energy output which the individual can exhibit in its life time," and that the "manner in which the environmental forces chiefly act in determining duration of life, appears to be by changing the rate of metabolism of the individual."

PHYSIOLOGY

Normal and pathological

The process of becoming can be illustrated also in more complex organisms and indeed in the physiology of man and in the changing susceptibility to disease which he manifests. It is perhaps unnecessary to refer to changes in structure which take place with advancing years. They are on the whole general knowledge and can easily be recognized. We refer here of course to the gradual changes in hair, eyes, and skin, to the alterations in the solid viscera and in the blood vessels; to the involution of the skeleton and of the muscles. It is not these so much as the changes which take place in function to which we desire to direct attention.

As an expression of the general activity of an organism the basal metabolism may be selected. We venture the opinion, in which Du Bois apparently concurs, that at all ages, but especially at the more ad-

vanced ones, more data are required before a definitive curve of change with time can be regarded as established. It is not only that more data are wanted; the conditions under which the observations are made need more precise definition. That there is a change in the course of life is clear from the results so far published. Benedict and Talbot, as quoted by Du Bois, calculate the basal metabolism in infants to be 26.7 calories per hour per square meter of body surface. In boys aged 6 to 7 years the rate is considerably higher, 57.5, according to Magnus-Levy. At 12 to 13 years it falls to 49.9; between 20 and 50 years it falls still lower to 39.7; between 50 and 60 years it is 35.2; and, finally, between 70 and 80 years, 30 (Magnus-Levy). The curve, it appears, begins at a low level, mounts rapidly, and attains its peak at about the age of 6 years; for 30 years it remains stationary and declines slightly and gradually thereafter. Here is distinct evidence that in the course of life fundamental changes take place. Precisely what changes is not yet known; undoubtedly they are significant but whether of the development of the muscular system in the early years of life as Krogh thinks, or of the activity of a specific growth stimulus resulting from the ununiform development of the glands of internal secretion is undecided. That it is possible to draw precise curves descriptive of change with age in the basal metabolism has been shown by Murray in the case of chicken embryos.

Curves of change in other general functions have likewise been drawn. Among these the blood pressure may be reckoned, representing as it does, not the result of a simple mechanism but a resultant obviously of a number of factors. Faber and James have made measurements in children from 4 to 16 years of age. In the curve for systolic pressure they assign 89 mm. Hg. as characteristic at the age of 4 years; 100 mm. Hg., at 8 years; and from here describe a more gradual rise to 115 mm. Hg. at 16 years. The diastolic pressure undergoes similar changes during this period, rising from 60 mm. Hg. to 67 mm. Hg. between 4 and 8 years and then more rapidly to 76 mm. Hg. at 16 years. From 16 years onward data are supplied by Alvarez. The curves which he has published represent probably the best standards now available, since they are free of the fault of selection inherent in those which have been commonly used and which issue from the examination of selected groups of individuals, such as applicants for life insurance. Although Alvarez's curves are based solely on figures obtained from university students they are representative of individuals in all states of health. For men at 16 years, Alvarez gives the systolic pressure as 127 mm. Hg., considerably higher than the figure of Faber and James; from this point to 30 years, the curve falls to 118 mm. Hg. In the case of women it begins at 118 mm. Hg. at 16 years and falls to 111 mm. Hg. at 24 years. After this, the curve again rises in the case of both sexes. If the curves described by Alvarez are correct—and they have to recommend them great care in the collection of the data—a new factor in the movement of the blood pressure with time emerges, namely, the fall in the curve between the ages of 16 and 24 years. The meaning of this change is still obscure and obviously requires further investigation for its clarification. For females, results similar to those of Alvarez have been published by Burlage. His figure, 104 mm. Hg. at 9 years, may be compared with that of Faber and James (101 mm. Hg.); at 14 years he gives 124 mm. Hg.; at 18 years, 114 mm. Hg. The last figure is to be compared with that given by Alvarez (118 mm. Hg. at 16 years) and

with Faber and James's (115 mm. Hg. at 16 years); at 26 years he gives 110 mm. Hg., to be compared with that assigned by Alvarez (111 mm. Hg. at 24 years).

Among the more general functions may also be placed immune reactions. Information on the relation of age to these is unfortunately not precise. But it is known in a general way that susceptibility to infection by several disease-producing agents is linked to age. Less importance must be placed on the fact that to certain of these diseases children are susceptible rather than adults who have attained the immune state than on the fact that children become infected by these illnesses at rather definite ages. Young children, for instance, are rarely infected by typhoid fever; and when it occurs in them, its course is mild. A similar statement may be made in the case of lobar pneumonia; and here again, the severity of the disease tends to be light. Young children are prone, however, to diseases of the exanthematous type. And again the incidence of rheumatic fever appears to be highest at 5 to 7 years (Ingerman and Wilson). It is a striking fact that children suffering from mumps are not troubled with orchitis as a complication until spermatogenesis has been established. (We are indebted to Dr. T. M. Rivers for this statement and for certain of the references which follow.)

Comparable information connected with immune reactions may be drawn from experiments on related matters in animals. It is stated that the skin of older guinea pigs is more sensitive to the action of diphtheria toxin than the skin of younger animals (Coca, Russell, and Baughman). The skin of the younger animals is likewise little if at all sensitive to watery extracts of tubercle bacilli; even though the regional lymph nodes and the spleen show evidence of the presence of the disease (Freund), while the skin of older ones readily shows this phenomenon. The nuclear inclusion bodies found in the testicles of certain monkeys, when inoculated with varicella virus, can be demonstrated only in young animals before spermatogenesis has been established, the reverse of the situation in the orchitis of mumps.

Of other more general functions such as that having to do with repair, little is accurately known in the case of man. Du Nouy has published information on differences in the rate of wound healing showing that this decreases with increase in age. In animals on the other hand more precise observations have been made. In rats, for instance, Mackay, Mackay, and Addis have found that after one kidney has been removed the other undergoes hypertrophy and does so the more, the younger the animal. At one month of age, the percent of hypertrophy is given by them as 52.6; at 3 months, 36.7; at 6 months, 32.8 and at 12 months, 32.2. That compensatory hypertrophy of the remaining kidney takes place was found also by Arataki. His experiments unfortunately do not contribute to the relation of repair to age. The rats he studied were all young, the groups being 20 days and 50 days old. On the basis of a life span of 500 days, these ages correspond to 3 and 7½ years in man; that is to say to ages at which sharp differences in behavior may not be expected to occur.

Several mechanisms of a more detailed nature than those to which reference has so far been made and in which a relation to the age of the organism has been shown to exist have been described. Gilbert recorded very simple but important observations on the change in effect which he noticed on the rate of the heart, when he pressed the vagus (the inhibitory) nerves in man. He found that with in-

creasing age the effect of this maneuver increases, that is to say, the rate of the heart decreases; and in a similar manner, that the interval between the time of contraction of the auricles and that of the ventricles lengthens out. Crawford studied a related phenomenon by observing the changing rate of increase of the heart following the injection of atropine. He found that the increase is maximal at 20 to 30 years, but that after this period the rate declines, at first slowly, but after 50 years quite sharply. In respect to both functions, then, time plays a rôle.

Studies of the vascular system have yielded data that illuminate the point that we are emphasizing. It has been found that change takes place in the degree of elasticity in human arteries. This change has been measured in terms of the velocity of the pulse wave and consists in a rise during life. Friberger found that in normal persons the rate between 16 and 25 years is 7.9 meters per second; and between 26 and 33 years, 9.2 meters per second. In persons in whom the arteries are thickened, the figure is a little higher, being 8.2 meters per second between 16 and 25 years; 9.4 between 26 and 33 years; the same between 45 and 55 years; and 10.1 over 55 years. Bramwell pursued this phase of the matter further with a more accurate technique. He found that a smooth curve might be drawn expressive of the experimental data. According to his curve the mean velocity is placed at 5.2 meters per second at 5 years; 6.2 at 20 years; 7.2 at 40 years; 8.0 at 60 years; and 8.55 at 80 years. These results are lower than Friberger's. But the point of interest is not the absolute figure but the fact that curves can be drawn illustrative of the general view we are maintaining that functions change with time. Daly has recently published data on a related subject, in this instance dealing with dogs. He found the "potential capacity increment," by which he means the extra amount of blood that the arterial system can take up, is large in young animals as compared with old ones.

When the blood itself is examined a number of interesting facts come to light. To begin with, the white cells change conspicuously in number, as Addison and Richter show. At birth they number between 17,000 and 18,000 per cc; a week later they fall to 15,000, and in adults they fall still further to between 5,000 and 10,000. In albino rats the course of events is strikingly different. Here, instead of falling, they rise with time. On the 18th fetal day, they number about 1,000; there are 2,000 at birth, 5,000 on the 5th day, and 8,000 at maturity. The red blood cells also change, decreasing in man from seven or eight million at birth to four or five million at maturity. In albino rats the change is again in the opposite direction, for in them on the 18th fetal day there are two million red cells, three million at birth, and seven to nine million at maturity.

Aside from formed elements other constituents of the blood, notably hemoglobin, undergo quantitative change. Whipple has shown in dogs that at 1 month the content is 50 mgm. per 100 cc, and at 1 to 5 years, 120 mgm. Between 10 and 12 years there is a slight fall to 110 mgm. The changes in muscle hemoglobin are much more striking. Heart muscle, for instance, contains 100 to 200 mgm. per 100 grams in the first few months; at 8 to 9 months, 300 mgm.; and between 300 and 400 mgm. when the animals reach adult life. Unfortunately neither the water content nor the total dry substance is given.

An interesting report is that of Bürger and Schlomka. (This publication came to our notice after the preparation of this

report was complete.) Like us they are interested in distinguishing normal from pathological processes in the course of aging. They selected for study especially tissues in which the rate of metabolism is slow and, as typical of this group, the cartilage of human ribs. This tissue loses water to the fourth decade; nitrogen apparently increases, in consequence, for its relation to dry substance remains constant. Cholesterin, however, actually increases; and so does calcium. These changes, as well as those seen in the cornea and in the walls of blood vessels, are the physiological result of aging and are not to be regarded as abnormal processes.

Differences have been described also in the chemical constituents of the blood. Tisdale and Harris, for instance, have found that at about 16 years phosphorus falls from 5.4 mgm. per 100 cc. serum to 3.8 mgm. Should rickets occur in early years the phosphorus level may fall to 3.0 mgm.; and conversely, in case of the fracture of bones in adult life, its amount rises toward the early high figure of 5.4 mgm.

Age also influences the amount and behavior of sugar in the blood. The basal amount averages according to Punschel 0.094 per cent between 16 and 34 years, 0.106 per cent between 58 and 70 years, and 0.110 per cent over 70 years. If 20 gms. of sugar are given by mouth, the quantities in the blood rise to 0.137 per cent, 0.153 per cent, and 0.163 per cent respectively at these ages; that is to say, the rise is greater the greater the age. Hyperglycemia follows ingestion. The period during which this state can be demonstrated to persist also varies with age. The figures are found to be 76 minutes, 99 minutes and 109 minutes; if 76 minutes is made to equal 100 per cent, 99 minutes equals 131 per cent and 109 minutes, 144 per cent. Hale-White and Payne found different figures but likewise concluded that the content of sugar in the blood varied with age, that its level was the higher the greater the age, and that the older the subject the longer did hyperglycemia persist after its ingestion.

In chickens, Baker and Carrel have found a relation to age in the content of lecithin and lipoid in the blood. The concentration of these substances increases, but cholesterol decreases with age. Hanes has shown likewise in chickens that the character of fat in the liver changes conspicuously during the embryonic period. During the first two weeks there are for the most part lipoids in which phosphorized fats predominate. These are isotropic. Later the character of the fat changes. There are instead esters of cholesterol, which are anisotropic. This metamorphosis is apparently associated with the process of calcification taking place elsewhere in the organism in the course of which phosphorized fats supply phosphoric acid. In rats, Falk, Noyes, and Sugiura describe progressive changes varying from 3 days before birth to 3 years 15 days. They measured concentration in terms of the ester hydrolyzing and lipase actions exerted by extracts of whole rats. The action increases from 2 days before birth to 126 days; finally in old rats at 1110 days there is a return to the behavior noticed at 27 days.

This bare catalogue of facts has an interest apart from its mere recital. The collection of such facts and others of a like nature should provide a basis for arriving at a more satisfactory notion of the mechanism underlying the aging process. To the readily recognized changes in morphology, especially in man, of which daily experience makes one easily aware, attention need not, as we have pointed out, be directed. Nor is it necessary to do so in the case of such

physiological phenomena as are representative of the sexual life, especially in women, nor to the change from feebleness to vigor in the young and again from vigor to feebleness in old age. But of the changes either in structure or in function which lie behind these manifestations there can scarcely be said to be more than a beginning of exact analysis. It is mechanisms of this nature which the present series of investigations is designed to analyse. The publications called Physiological Ontogeny (Jour. Gen. Physiol., 1925–26. ix. 1–37, 39–48, 405–432, 603–619, 621–624, 781–788, 789–803; 1926–27. x. 337–343. Jour. Exper. Med., 1925. xlii. 275–290, 291–297, 299–310), some of which have already been published and to which this essay serves as an introduction, illustrate the viewpoint from which this investigation is being pursued. It is not difficult to see what are the sources of our interest in this matter. The facts of course have an interest on their own account, apart from the satisfaction that comes from bringing a greater measure of order into what appear to be unrelated phenomena. The more exactly they are collected and the more extensively they are correlated with other phenomena, the more clearly will emerge the conception that the study of physiology must consider mechanisms not only as they appear at a fixed period in the life history of an organism but must extend its view to embrace in its descriptions the changes which take place from birth to death. For an analysis of a function which is correct and complete during adolescence need no longer be, and indeed often is not, descriptive either of maturity or of senescence. In this view physiology will become the description, not of a point, but of a curve. It will be a matter of singular advantage to possess curves of normal form and of normal behavior coextensive with the span of life. These will facilitate judgment of what are average manifestations of life, year by year and decade by decade. In the domain of medicine we shall be classifying quite differently phenomena which now pass as evidences of disease. Many of them we shall be recognizing as appearances characteristic of the senescent or of some other normal state. How far reaching a change in orientation may take place in the practical world of medicine in consequence of a realization of the meaning of new definitions, it is not possible to do more than to suggest. But one can foresee that there reside implications in this outlook which are significant for the future of research and for the application of therapeutics. In point of fact study in the process and state of senescence will suggest directions for research distinctly different from those devoted solely to the hope of preventing or of curing its manifestations.

THEORETICAL CONSIDERATIONS

We have reviewed what we believe to be the chief facts relevant to the problem of ontogeny in the domains of general and human biology, normal and abnormal. On the basis of these and other findings men have speculated about the "causes" of aging and have developed concepts to "explain" senescence and death. Various theories have been proposed engendering differences of opinion, some of which seem to have been due to a disregard of the fact that all hypotheses do not belong in the same category and for this reason may not be compared. Another cause of confusion is a prevalent belief that one factor to the exclusion of all others must be found to account for the phenomena.

It does not seem to be universally evident that the same phenomenon may be viewed in a number of distinct and mutually independent aspects. It is often

assumed that the most dispassionate quantitative description of nature is that made possible by statistical methods, a subject that we shall discuss later. But scientists, who in the end are human, have always interested themselves in causes; so that even now, despite Hume's logic, they proceed in their experimentation as if the doctrine of causation were a rational induction from experimental knowledge. Causal biological theories have fallen naturally into two categories, the mechanistic and the functional or teleological. The *mechanistic*, which entail the proverbial infinite regress, rest finally upon such convenient subjective concepts as force, energy, and affinity, whereas the *teleological* theories are directed towards the future, towards either (1) an ideal, living, perhaps anthropocentric goal, as in the case of the "survival of the fit" concept, or (2) a mathematical, esthetic, fixed termination, such as the "least action" law. These are so-called final causes.

From the standpoint of *efficient causation* the problem of ontogeny is exceedingly difficult. Many processes related mysteriously one with another are all occurring simultaneously. Which are the significant ones? One thing is now certain, that no clear understanding of the concrete fact of evolution can be reached from a one-sided approach.

Hitherto there seems to have been an undue insistence upon describing the life process in terms of some one variable, whereas it is possible that ground may exist for harmony between many of the theories recently in dispute. For instance, with the literature in mind, it may be said that life is characterized by an *attractive or integrating force* (Spencer), exemplified in the molecular sphere by an increase in the size and complexity of the protoplasmic units (Müller, Cohnheim, Bühler, Rubner) or more generally by a change in the "physico-chemical substratum of the cell" (Child). This leads to a concentration of solids (non-electrolytes), so that permeability (Benedict) and electrical conductivity (Osterhout) become diminished. As a result the velocity of chemical change is lessened, and consequently the nucleus, which is believed to be the regulator or organizing centre of cellular metabolism (Conklin), shows a special and relatively greater integration, as for instance in the decrease in the nucleoprotoplasmic ratio. Excretion becomes progressively less efficient, and the end-products of metabolism accumulate in the cell (Jickeli, Montgomery). In the cytoplasm, owing to the gradual cessation of motion with the accumulation and concentration of matter (Liebermann), precipitations or agglutinations of matter occur, giving rise to metaplastic granules (Mühlmann, Kassowitz). These still further limit metabolism and accelerate a vicious cycle.

In such a way it may be possible to weave together in a general, but to be sure rather vague, way the principal "causes" proposed as "explanations" of aging. Naturally, for certain purposes it is permissible to regard evolution in such terms as membrane permeability, colloidal flocculation, or nucleo-plasmic ratio, but these are necessarily one-sided views and inadequately descriptive. Since there is reason to believe that a knowledge of the successive *physico-chemical* states of the proteins in protoplasm would give us the best description of the fundamental changes with age in living tissue, frequent analogies to the aging of colloids are found in the literature. For instance some solutions, such as silicic acid, when freshly prepared are easily dialyzable but lose this power on standing. Small particles aggregate into larger units, which flocculate more easily or do so spontaneously. When unstirred, colloids

become more stable. Bechhold says that gels become less elastic and optically less homogeneous or turbid, and that a high temperature accelerates these changes. These are characteristics shared by aging tissue. Possibly division and reproduction of cells correspond to the preparation of a fresh colloidal suspension but, as with age cells divide with diminishing frequency, this freshening process is less frequent and, perhaps owing to the changing milieu, less complete.

As certain glands of the body have special functions in regulating growth, as for example the thyroid, thymus, pituitary, and gonads, and as the tissues of these parts must also undergo the above mentioned orderly modifications in constitution and behavior, their secretions must likewise change quantitatively with time. The discovery of growth or metabolism modifying principles in the blood serum or tissue juices, though of great interest, does not in any way change the nature of the problem. For since these activators and inactivators are themselves products of tissue dynamics, we are driven back to an investigation of the latter to account for the age changes in the concentration of the former. But the existence of this fact does not make futile, or any the less interesting, the search for special agents, for a part of the problem of mechanistic causation involves a search for these specially differentiated processes or areas that have dominance in regulating the velocity and nature of other vital activity throughout the body. As a result of considerations like these comes up the question of the leaders of the ontogenetic process—whether considered anatomically, cytologically, or chemically. Experimental embryologists have within recent years, following the guiding experiments of Spemann, shown that there is a hierarchial regional control in the body, that certain parts of inherent high potential control, even when transplanted to foreign parts, the activity and development of the cells around them. For instance embryonal skin cells of the abdominal wall are made to develop into a normal lens under the influence of optic cusp tissue transplanted into their midst. Jones calls this mysterious organizing principle, cytoclesis. Regions of dominance are seen to determine the activity about them and modify both the quantity and the quality of differentiation. There are innumerable instances also where one part inhibits the immediately adjacent parts, where one zone becomes suddenly marked out for growth and its surroundings are repressed in their activity. This fits in very well with Child's work in which he showed that in worms, dominance was associated with high metabolic rate, and that in some of the lower forms he could distinguish so-called metabolic gradients, forming an axis, the structural characteristics and physiological phenomena being also related to this axis. Lillie believes that these apical active regions are negative to the basal, less active parts. Bioelectric currents are in consequence set up which may have an influence on neighboring parts even when there is no tissue continuity between them. On this plan we find a metabolic hierarchy in the microcosm, the mainspring being the point of high oxidation or the independent variable in the developmental process.

To other investigators similar ideas on the order of phenomena have appeared to be relevant in the domain of chemical activity. For in successive chemical reactions and in the accompanying redistribution of elements, some substances apparently have greater mobility, greater permeability, and a greater migratory rate than others. Viewed from these

several angles the idea seems to gain force that one constituent takes the lead in the evolutionary process, whereas the others show relative degrees of lag.

If, when a complex equilibrium is disturbed, one of the elements is found to move with the greatest velocity to reach in the shortest time a second relatively fixed state, it does not signify that that element is the "cause" of the chemical reaction. For instance, because CO_2 diffuses faster than O_2 through the pulmonary epithelium, need it be considered more than a link in the respiratory gas cycle? And again, because in the electrolysis of sodium chloride the migratory rate of $Cl-$ ions is greater than that of $Na+$ ions, are we thereby to understand that the electrical phenomenon is "caused" by the chloride ions? Such considerations are relevant to the evolutionary differentiation of protoplasm, in the course of which some constituents reach steady states before others, and so the phenomenon of molecular change in the presence of a more or less constant milieu is found.

But in any case it is clear that the ontogenetic process is no simple affair, no matter which chemical leadership or master-reaction develops during any one period, nor should one expect any determining leadership to last. The sudden emergence of a mutant reaction or novelty should be expected as a frequent occurrence during ontogeny. We are prepared to find that new substances and new forms spring or are forced into being when the milieu provides the necessary and adequate conditions.

One of the most satisfying theories to account for organic aging was, it seems, first proposed by Spencer, and later widely discussed and accepted by others. It called attention to the changing relationship between surface and volume as the necessary concomitant of growth. It is in the very nature of geometric relations that with growth the volume or mass increases as the cube, and the surface as the square of a number. The result from a biological standpoint is that for a unit mass of active protoplasm undergoing continuous chemical changes, the portals, that is to say, the surfaces of the organism for entry and exit of the substances which are the antecedents or products of vital activity become continuously smaller, and therefore continuously less suitable for maintaining the original velocity of metabolism. There must necessarily follow a diminution of activity and all the other changes that are merely the logical outcome of the initial modification. This may prove to be the crux of the problem, all the important surface areas of the body, skin, gastro-intestinal, renal, pulmonary, cellular, and molecular, being nicely, mutually balanced to one another, and organically adjusted to the metabolic rate. This argument depends on the analogy which has been chosen, namely, the properties of the sphere. There is presumably nothing to prevent the surface of an organism from attaining any area regardless of its mass, by the development of infoldings for instance, unless it be the principle of efficiency which would dictate an approximation to the spherical state. A relatively large surface is a great expense.

There is, however, another approach to this problem, apart from mechanistic theories; the successive stages of an individual life cycle may be examined and described in *teleological* terms. Instead of attempting to "explain" the changes with age in terms of established physicochemical laws, one can enquire: What purpose do they fulfill? What part do they play in maintaining in the organization the stability and thus the integrity

of the individual? In what way do given changes increase survival value? This viewpoint is in no manner contrary to mechanistic concepts, but may be used as corollary to them. For instance, Weismann's notion, to the support of which Pike has recently come, that individual death is an inherited characteristic that has become fixed by natural selection, is a teleological theory, arising from considerations of racial interest. Pearl, evidently believing that the acceptance of this view would tend to destroy the validity of mechanistic principles, has said that "probably no more perverse extension of the theory of natural selection than this was ever made." But Pearl himself believes that death is the result of differentiation, that "natural death, as distinguished from accidental death, is preceded by definite structural and functional changes in the body." It follows that death is the final senescent state. Senescence is in short a process innate and inherent in the life of protoplasm. Then since, as Pearl himself seems to admit, senescence (that is to say natural death) and somatic differentiation are positively correlated, never independent, and hence for the purpose of this argument synonymous, Weismann's statement amounts to little more than to saying that somatic differentiation has survival value for the race. The soma itself, since it cannot give rise to new individuals, must perish. Life after reproductive functional atrophy has become established represents the reserve capacity or margin of safety for continued existence which is commonly found in nature. In imagination we may reconstruct a picture in which at the moment of emergence of metazoan from protozoan life competition between the wholly immortal protozoa and the partly immortal metazoa took place.

The metazoa have survived the struggle; their plan of organization provides for soma and germ plasm. For germ plasm there is unbroken descent down the ages, but for the soma, individually and elaborately differentiated though it is, there is only a series of successive deaths. Procreation is the crucial function; the soma is in this sense superfluous. This seems to have been Weismann's meaning, and Pike's. There can be little doubt that the motive for the belief that the preservation of life is of paramount importance has an anthropocentric origin; that the mechanisms which are concerned in bringing about survival of the soma have intuitively become the subject of major interest. There seems to be a directive tendency in organic phenomena which lends color to man's inherent wishfulness. These he names reactions, reflexes, instincts, and pre-dispositions. Nature's goal seems to correspond to his own. Natural phenomena may, therefore, be investigated in the light of this goal as if they had a function for a telos, that is to say, for the preservation of organic existence.

There is still another group or type of explanation for the life process also to be classed with final causes. These point out that there is a tendency on the part of mechanisms to move toward some final condition or fixed state. These have an esthetic motive and are derivations of or analogous to the Second Law of thermodynamics. Aristotle was not far from the general idea of degradation when he spoke of the innate heat existing at birth and of its gradual dissipation during life, a phenomenon which was responsible for senescence and death. Thermodynamic reasoning applied to ontogeny yields approximately the same result; the terms according to which the argument proceeds make little difference, whether it is of change from instability to stability or from

the homogeneous to the heterogeneous, or whether the appeal is to the concept of organization or to the principle of least action. In all, increase in entropy, or death, is the final state. But if the universe were governed solely by this principle, why, since time is infinite, is there, as Boltzman has asked, any free energy left in the universe? And the answer must be that there is another principle of an opposite and compensating character, a principle still hidden, which from its nature may be forever hidden from scientific investigation. Chvolson's statement that "the second law is the law of evolution of the world accessible to our observation," is in accord with the facts of ontogeny as we know them. The natural history of an organism from birth to death is the change from greater to less chemical activity per unit mass compatible with life. In the case of the ameba there is a periodic phase of reversibility associated with division, in which there is a complete return to the initial condition of high polarity and metabolism. From this point of view sexual and asexual reproduction are essentially the same. The act of creation synthesizes the lost energy. It is as if fertilization explosively and mysteriously lifted a pendulum to its highest summit and the rest of life were the story of the gradual decrease in the amplitude of its swings. In this sense the law of the degradation of energy describes the life process itself; it satisfies mathematical, esthetic, and sensational predispositions. Other descriptions would arise satisfying to psychological, emotional, and action values. The action would be interpreted in terms of reaction. The gradual fall of the pendulum would represent a direction towards the succeeding lift. The ameba hurrying through his life cycle would be ever approaching childhood, that is to say, redivision. We do not escape from our fundamental motives; these two human tendencies creep into scientific outlooks. In the ameba, the mortality of the individual as an integral unit is contrasted in most striking terms with the immortality of the germplasm. Has science any explanation for the rejuvenescence occurring with fertilization? How is the initial energy restored to the daughter cells? On the inability of science to cope with such questions vitalists have thrived.

In reviewing the hypotheses and generalizations of later biologists one is impressed by the fact that since the days of Herbert Spencer very few important biological conceptions have been contributed to modify his system. Evolution, of which ontogeny is a particular example, in his view "was an integration of matter and concomitant dissipation of motion, during which the matter passes from indefinite, incoherent homogeneity to a definite, coherent heterogeneity; and during which the retained motion undergoes a parallel transformation." This statement has close suitability to the statements of later observers, namely, that development is characterized by an increase in size or growth, a decrease in chemical activity or metabolism, a differentiation and specialization of form and function, and a more efficient organization resulting in greater internal uniformity and stability.

Since Spencer's original formulations the most significant contributions germane to our problem have been:

(1) The distinction between cells organized into an individual whole (a multicellular organism) and unorganized cells, that is to say cells with no collective function, as in the case of unicellular organisms, tissue cultures in vitro, and tumor cells. For these advances Galton,

Weismann, Woodruff, Jennings, Harrison, Carrel, Leo Loeb, and others are chiefly responsible.

(2) Experiments showing the nature and significance of dedifferentiation and rejuvenescence in the life cycle (Child).

(3) The factors influencing the duration of life (a) inherited and (b) environmental, elucidated by the work of Bell, Pearson, Pearl, and Jacques Loeb.

(4) The concept of emergent evolution (Lloyd Morgan) and

(5) The principle of organization and the concept of organism as developed by Henderson and Whitehead respectively.

The most comprehensive recent generalizations to describe development and senescence have been made by Child. He states that "senescence is primarily a decrease in rate of dynamic processes conditioned by the accumulation, differentiation, and other associated changes, of the material of the colloid substratum." This statement is very similar to, but somewhat less descriptive and comprehensive than Spencer's dictum.

There is still another, and in this summary, final approach to our problem, independent of all preliminary intuitions about efficient and final causes, and that is the method of quantitative description by statistical analysis. Death is the endpoint of an aging process of the greatest possible complexity, which starts at birth. From what was said in the discussion of efficient causes it is clear that aging cannot be described in terms of one function. The most adequate account, as Müller predicted long ago, is the measurement of co-existences. The methods devised by Galton and elaborated by his followers make it possible to carry on this method in a systematic quantitative fashion. The nomographic method applied so successfully by Henderson to the study of the blood stands as a successful typical example for physiological description. For ontogeny the greater complexities of the living organism and the introduction of another dimension, Time, increase the difficulty of the problem. The omission of significant factors makes the description inadequate, the inclusion of irrelevant matter makes it cumbersome. This method, though tedious, seems to offer the best prospects of unearthing the more significant correlations and hence of discovering the fundamental physicochemical changes, which would presumably provide a basis for a better understanding of the evolutionary process. Pure description has often been the necessary preliminary to "explanation" or has often by itself been regarded as the "explanation."

EXPERIMENTAL CONSIDERATIONS

Reflection upon the facts and theories reviewed, however briefly, in this paper, leads naturally to a belief in the importance of a comprehensive investigation of the same organism simultaneously undertaken from a number of distinct standpoints over the entire ontogenetic period or at least over a certain specified portion of the life span. A study so planned seems especially significant when the present day trend of biological interest towards an examination of the togetherness or totality of the organism is appreciated.

This statement applies no more to the whole organism than to any one of its parts, the heart for instance, which may specially concern the investigator. Heart muscle, as a representative tissue, is especially suitable for a number of important physiological, chemical, and physical measurements. A study of its energetics in relation to senescence seems, moreover, to be the first logical step in the further elucidation of the problem of chronic heart disease.

The extent of the duration of life of

many living forms necessitates at least a preliminary concentration upon some one period of the cycle. Usually there are three periods, embryonic, infantile, and adolescent, which are characterized by accelerated evolution and which for this reason offer the most appropriate conditions for systematic observation. Of these three periods the embryonic is by far the most important, both because during this time the changes are many times more pronounced and easily measurable, and because of the phylogenetic references.

Long ago it became evident that the Biogenetic Law, which states that ontogeny follows phylogeny, was untenable, for it was noted that each new development or emergence could not be forecast from the very beginning and that each ontogeny showed variance in every stage. The two series, phylogeny and ontogeny, stand nevertheless as crudely analogous phenomena, and, lacking a complete paleontological record for any one species, ontogeny may be taken to present the best record that we possess of racial trend.

Tangl has pointed out that the water content of the organism decreases with development both in phylogeny and ontogeny; and it appears that such is also true for the calorific value per unit mass of tissue. Does the sudden desiccation of the tissues during the growth of the embryo correspond to the emergence from aquatic life? This and other questions of a like nature present themselves and emphasize the peculiar importance of the embryonic period.

The difficulty of physiological experiments upon mammalian embryos led us to choose the egg, or more specifically the chicken embryo, as the object for study. A number of other unforeseen advantages presented themselves, among which may be mentioned the fact that (1) the environment, consisting of the surrounding atmosphere and the food supply of the embryo, that is to say the yolk and albumen, is relatively stable, (2) the age of the organism may be closely estimated, (3) the initial poikilothermal and eventual homoiothermal nature of the chick allows for an investigation of temperature effects and of the development of a mechanism for internal control, (4) the embryos are sterile, a fact which enhanced the facility with which various operations, such as tissue cultivation, could be performed, (5) the supply of fertile eggs from hens of the same breed was plentiful and sufficient at all times for our needs, and (6) the chicken embryo has always played a leading rôle among the objects of biological investigation. Aristotle, Fabricius, Harvey, Malpighi, John Hunter, and Haller, it is known, made studies upon its development, Wolff used it for microscopic examination when he overturned the firmly rooted theory of preformation, and since the latter's day it has been studied by embryologists more intensively than any other species.

A knowledge of form is important to parallel the physiological studies, since the problem of the functional equivalence of structure depends upon correlations between the two. The change in character or value of each function as incubation advances and the rate and acceleration of the change will be matters of interest and phenomena for comparison. Heretofore interest has not been sufficiently directed towards the question of velocity, except when concerned with the problem of growth. It has been stated that with age changes such as dehydration and decrease in the heart rate occurred but never at what rate these took place. This conclusion has often been reached by comparing values at the two extremes of life. The advantage of knowing the

values intermediate between the extremes is that rates of change at different ages may be represented by the slopes of the line connecting the points, and thus the dependence of functions changing at similar rates in respect to age may be made evident. It will be found, as Lotka states, that the most important expression is not the quantity of any one factor at a given time, but rather the rate of change of that quantity at the time. In this connection it may be well to point out that rates of change will not be found uniform at all times for all tissues in the organism. It is in fact already well known, crudely, that tissues and organs exhibit changing relative significance with time and that this is reflected in their morphology. Equal growth may be designated symmetrical; unequal, asymmetrical development. We have already referred to this phenomenon in another connection (physicochemical activity); it seems not unlikely that it will play a part in our future studies.

This review is designed to present the facts and opinions found in the literature dealing with the aging process and is intended to indicate the rational considerations that underlie the investigations that have already appeared or are in process of publication.

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PLANT WATER RELATIONS

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INTRODUCTION

PERHAPS no subject in plant physiology has been discussed at greater length than the problem of the rise of water in trees. The literature of this subject has been increasing since the appearance of Stephen Hales's *Vegetable Staticks* in 1727. It is now enormous. Some phases of the earlier scientific discussions have filtered out into the realm of popular knowledge, and intelligent people everywhere are now at least aware of the existence of a peculiarly interesting problem in this connection. The ascent of sap constitutes a subject of perennial interest to many minds that are not specially devoted to plant physiology or even to any branch of natural science. The more fruitful contributions toward an appreciation of this very fundamental natural process are, however, of recent date, for what now seems to be the basic clue to the mechanics of the rise of water in trees did not get adequately presented until the appearance of Dixon's publication in 1909. Study in this field has gone on with renewed vigor since that time, and the general principles involved in the "transpiration stream" appear now to be fairly well worked out. But these recent results have not yet reached the intelligent public; indeed, they are only beginning to be presented in school and college text books of botany, and their implications are but vaguely envisaged by many professional workers in plant physiology. Popular science and school and college science must generally lag very much behind research, but in this case the lag is remarkably great.

The physical explanation of the rise of water in trees now leads far beyond this movement itself, to problems of the entrance of water into the plant body on the one hand, and, on the other hand, to those of water retention within the plant and of water loss. Tall trees furnish an obvious example of certain apparently somewhat uncanny phases of plant water relations, but forms of low stature generally present the same problems.

From a less philosophical point of view the subject of plant water relations is of interest to all who have to do with living plants, which implies almost everybody. I may mention agriculture as the great, fundamental human occupation and then proceed to note how important water is in crop production. As the earth is constituted, water and temperature—the water supply and the heat supply—are the main limiting conditions that demark vegetational and agricultural regions. Water conditions of crop plants are readily amenable to artificial modification. Recent advance in our knowledge of how plants need water and why some forms need more to produce a crop than others has led to great improvement in irrigation and drainage. Also, attacks of fungus and insect parasites on cultivated plants are found to be related in many cases to the moisture conditions of air and soil.

In the following pages I aim to present a

general outline of plant water relations, according to the present state of knowledge. The complexity of the subject and the intricate inter-relations of the various topics that require attention render the organization of such an outline somewhat difficult and compel more or less repetition in the interest of clearness and readability; in an essay of this sort the same elementary principles need to be considered from several different points of view. I am purposely leaving out of consideration many details that remain still to be elucidated, over which discussion among specialists is now going on. Other details that seem to be fairly well understood are omitted in order that the main features may be more clearly presented. Attention is here confined to ordinary vascular plants, with root systems in water or soil and with stems and leaves in air.

The literature references given at the end of this article are calculated to place the reader in touch with some of the most useful discussions of the various topics. The very extensive literature abounds in curious vitalistic or mystical conceptions and implications, and physical principles of great variety (both real and imaginary) have been wrongly or inadequately invoked from time to time. Such material is generally left out of the present picture; it is mainly historical now. A large number of additional references to the literature, some of which may well be fully as important as many that are actually given in my list, will be found in the papers and books that do receive mention here.

THE GERMINATION OF THE SEED

The resting embryo may be regarded as a complex mass of colloidal substances containing but little water and but little dissolved material. It is structurally divided by the cell walls into apparently distinct little regions or chambers, the cells. The cell walls themselves are ultra-microscopically porous, like gels, and contain some water, held very firmly in the pore spaces by the adhesion or attraction forces that hold water in close contact with most other substances; in a word, by imbibition. According to the nature and distribution of their non-water materials, some walls contain more water than others, but we may think of them as all in water equilibrium with one another, all being as nearly saturated as the meager supply of water in the resting seed permits. The cell contents are also colloidal gels impregnated with water of imbibition, which are in approximate water equilibrium with the walls. Water is held in the walls, protoplasm, starch grains, etc., by the complex of adhesion pressures just mentioned.

In the cell cavities osmotic attraction for water is also active to a high degree in many cases, for much of the water-dissolved material of the vacuoles is greatly hindered or practically prevented from outward diffusion by osmotic membranes that line the cells. The layer of protoplasm lining the cell is nearly or quite impermeable to the osmotically active substances of the vacuole, although, like the walls, it is relatively very permeable to water. Solutes that cannot diffuse out into the walls generally develop, therefore, considerable osmotic pressure. In the embryonic tissues, whose cells have no large vacuoles, the cell cavities are filled with the protoplasmic gel, in which a considerable water content is held, partly by imbibition and partly by osmotic attraction. When the water-attracting materials are in solution and the solution is retained by superficial layers or membranes that prevent or greatly hinder the outward movement of the solutes, the attraction is osmotic; when the

particles whose surfaces hold the water are not dissolved their attraction is imbibitional. This distinction, somewhat artificial as it may prove to be, is worth while because osmotic attraction of solute for solvent is much better understood than are the attractions that tend to hold water on surfaces of materials that are not dissolved. Both kinds of pressure are probably present in nearly dry protoplasm, but osmotic pressure is surely the important feature of water retention in vacuolated cells. Most of the study of water retention by plant tissues has been based on the supposition that it is due to osmotic phenomena, and imbibition has not received much attention.

The outer layers of cells in the seed are mainly without protoplasm or contain but little. Their cell cavities are small or filled with gas, their walls are generally so made up that they hold very little water when saturated (somewhat like blotting paper that has been impregnated with varnish and then dried), and they greatly retard evaporation of water from the seed. In some cases they are almost impervious to water movement either outward or inward, even when the seed is submerged in liquid water. Some seed coats must be broken or punctured before water can enter rapidly enough and in sufficient quantity for germination.

When a seed is brought into contact with liquid water the imbibition and osmotic attractions cause water to enter. The cell walls swell more or less, as their pores are enlarged by the entering water, and the cell contents also swell. A limit to the swelling of walls is soon reached, when the cohesion of the gel (cellulose, etc.) is just balanced by the imbibition attraction. Contents of living cells are capable of much additional water absorption, but they cannot escape through the walls; as water enters, the walls are stretched until their elasticity balances the combined osmotic and imbibitional pressures acting outward from within. The cells thus become turgid and resist compression and deformation much as does an elastic solid. A turgid cell behaves much like a sheet-rubber bag (such as a foot ball) into which water has been forced until the rubber has been somewhat stretched and pressed firmly against an outer, less extensible, enclosing wall. The ordinary foot ball or automobile tire is turgid because the high internal gas pressure stretches the thin lining, forces it against the casing, and stretches the latter till its elasticity balances the distending pressure.

While the seed swells, and throughout later stages also, chemical and resulting physical changes go on in the embryonic cells. Dissolved substances like sugar and salts get transformed in complicated ways, and new protoplasm is added to what was originally present. As imbibing and osmotic material increases in a cell, more water is drawn in from the surrounding tissue (if the resistance to water absorption is not too great) and finally from outside of the seed. The whole mass of the seed, walls and cell contents alike, tends always to reach water equilibrium throughout and also in relation to the surroundings. Water moves from places where osmotic and imbibition attraction is lower to places where it is higher. The embryonic cells consequently enlarge, their walls become increasingly stretched, and the latter would be ruptured but for the fact that the metabolic processes add wall material that continually counteracts the effect of stretching. The enlarging protoplasmic masses divide, new walls are formed across older cells, and the smaller cells thus formed repeat the process of swelling and division.

THE SEEDLING

The embryo becomes a plantlet, and the plantlet becomes a plant. Non-water material is added at an adequate rate, and this addition controls the rate of water entrance, assuming an unrestricted external supply of water. But the amount of non-water material (such as sugar, salts, cellulose, etc.) requisite for a given amount of tissue enlargement is very small compared with the amount of water required. Enlarging tissues, and active tissues generally, are mostly water, to within a few points of one hundred per cent, by either weight or volume. The source of the necessary water is at first the liquid bathing the seed, which enters through the seed periphery. But roots soon protrude and add greatly to the extent of the absorbing surface, and consequently to the rate at which water can enter the organism, if only their enlarging external surfaces are kept wet.

The material used in growth, other than water, comes at first from the accumulations in the seed. Later the supply comes largely from sugar that is formed in the leaves through photosynthesis, but salts enter with the water, though at independent rates. It is interesting to note that the products of photosynthesis are formed from water and carbon dioxide and that a certain rate of water supply is therefore required even for the production of the osmotically and imbibitionally active substances and structures that attract the entering water. Some water is chemically used up in the formation of the very machine that brings in the supply needed for enlargement. On the other hand, and from the very first, water is chemically formed in the organism at a low rate through respiration and related processes, especially in active tissues. In aerobic respiration oxygen from outside of the seedling is consumed in this way. For later phases of development much of the oxygen supply for aerobic respiration may come from the photosynthetic process in illuminated green tissues. This small internal supply of chemically produced water may in some cases be quantitatively important for the growth of young seedlings not adequately supplied with water from without.

We may now suppose that our plantlet has the ordinary outfit of roots, stem, and leaves, and that the stored material of the seed has been used up. For the sake of simplicity let us suppose that the roots are in a suitable dilute salt solution, that they are submerged in liquid water. For the type of plant we have in mind the leaves are in air, and the stem connects them with the root system. The whole organism is a mass of water held in place and in shape by a remarkably small proportion of other materials, to which the water is attracted, to which it adheres. The detailed arrangement and nature of these other materials determine the form and size of the plant at any time, also its structure and its ability to retain its water against the action of forces that tend to attract water outward or to press it out.

The outer layer of the plant is finely porous cell wall impregnated with water of imbibition, and the extent of the external exposure of liquid water thus established is determined mainly by size and frequency of the ultra-microscopic pores. Some peripheral surfaces expose their imbibition water rather freely, as in the case of most young roots and root hairs; others present almost no water to the surroundings, as in the case of the epidermis of a cactus stem or the leaf of an India rubber plant.

In the interior of the plant body innumerable water-impregnated walls surround and join the living cells. These

cells are lined with osmotic membranes that tend to hinder or prevent the outward movement of osmotically active solutes, and the water of the vacuoles is thus retained by osmotic attraction. Each cell is turgid and acts as a very elastic solid, as has been said. The walls are stretched and elastic, but not stretched to the limit of their tensile strength; there is generally some extensibility to spare, and the tissue may therefore be bent or otherwise deformed to a considerable extent without rupture. But very turgid tissues with very weak walls are really brittle, as in the case of very young shoots, the pods of prime stringless beans, etc. The protoplasmic linings of two adjacent cells are, in many cases at least, made continuous by plasmodesmi, intercellular protoplasmic plugs of microscopic diameter, which occupy corresponding microscopic openings in the intervening wall.

Besides the living cells there are other spaces or chambers within the plant body, not filled nor even lined with protoplasm, but entirely surrounded by water-impregnated walls just as are the living cells. Some of these represent dead cells. Typical vessels, which extend from root to leaf in the vascular bundles, are linear series of cells from which the original protoplasm has disappeared and in which many of the cross walls have been wholly or partly removed by digestion. They are essentially long, narrow tubes with relatively infrequent cross septa. Septa and walls are water impregnated, and the lumina are at first filled with water (aqueous solution) and eventually with gas as they become old. Many other kinds of dead cells, generally filled with gas, occur in old stems, such as trees. Other chambers besides living and dead cells are the intercellular spaces, usually gas-filled also. These are formed by splitting of walls and pulling apart of the two resulting layers. Intercellular spaces are in many cases very extensive and complex in form as a result of the "running together" of many adjacent spaces. They may open to the exterior, as through stomata and lenticels. The cavities of dead cells and of intercellular spaces may be joined by the disappearance of a portion of wall.

Liquid water is seen to be continuous throughout the plant excepting for the gas-filled chambers, which are somewhat like gas bubbles in a free liquid; only they are held in position and size and form by the relatively rigid water-impregnated walls about them. Where several gas-filled spaces are adjacent the imbibed water held in the intervening walls is of course in vapor-pressure equilibrium with the water vapor of contiguous cavities. These walls are not nearly dry, excepting when their pores are largely filled with wax-like substances. The plant is therefore, as I have said, essentially a mass of liquid water held in a characteristic nexus of porous cell walls by the attractions of imbibition and osmotic pressure. It retains its form in spite of the influence of gravity, wind, and other deforming agencies, mainly through turgor in the young parts, but in thick walled tissues through mechanical resistance of wall material. Turgor involves the tensile strength of the walls and their tendency to contract when slightly stretched by outwardly directed turgor pressure; this is generally osmotic but may be partially imbibitional if the swollen protoplasmic gel acts, as a swelling colloid, to stretch the walls. In some older tissues (like wood and sclerenchyma; consider ordinary wood and the stone-cells of the date seed, etc.) the very thick walls themselves resist compression as well as other forms of deformation to a great degree.

In tissues of thin-walled living cells

(such as celery or rhubarb petioles and young leaf blades, as well as many kinds of mature leaves and even stems, fruits, etc.) the whole structure shrinks markedly and droops when turgor disappears. We say the tissue wilts under these conditions. Wilting properly begins when the cell walls cease to be stretched by turgor pressure. It may be brought about in either of three ways: (*a*) By depletion of the osmotically held water in the cell vacuoles (in which case the volume of the osmotic solution decreases, its concentration and osmotic value increase, but the actual osmotic pressure, or turgor pressure, decreases). (*b*) By the removal of osmotically active solutes from the vacuolar solution, as when sugar is converted into starch and water (in which case the osmotic value of the vacuolar solution decreases and consequently the turgor pressure that tends to stretch the walls). (*c*) By the escape of osmotic solution from the vacuoles, as when the protoplasmic cell lining becomes more permeable to some or all of the osmotically active solutes (in which case the turgor pressure decreases, although the osmotic value of the solution may be unaltered; an illustration may be had by killing the protoplasm in a turgid leaf, as by boiling).

Through the imbibition water of the peripheral cell walls the water mass of the plant is in direct contact with the environment, and water (and substances soluble in water) may enter the plant or leave it across these interfaces. According to the nature of the external walls, whether cuticularized or not, etc., the interchange of water between the plant body and its surroundings may be very much hindered (cuticularized, suberized, etc., walls) or may be relatively free (walls of substomatal spaces, root hairs, etc.).

Also the cell walls throughout the plant interior vary in water content and in the resistance which they offer to the movement of water through them, but all are impregnated with water. As to the chambers, all living cells exhibit continuous water from wall to wall, as do also many kinds of dead cells, especially the vessel segments while they are relatively young. Because of the continuity of liquid water, a solute particle might enter the plant at any point, by becoming dissolved in the pore water of an external wall, and might then diffuse across walls and water-filled cavities to any other point in the plant, remaining all the time in solution. (Such a particle might pass out of solution at some point on the periphery of a gas-filled space, diffuse across the space as a gas particle, and enter the liquid phase again at another point on the periphery of that space.) Such diffusion of dissolved substances may occur slowly from any part of the plant to any other part, provided none of the colloid layers encountered are impermeable to the diffusing particles.

But the resistance or retarding effect of the innumerable colloid layers (water-impregnated porous walls and the protoplasm of turgid cells) is very great, and diffusion from place to place in the plant must therefore be very slow indeed, much slower than would be the case in perfectly free liquid water. Solute diffusion through free water is itself very slow, but what appears as diffusion in that case is generally greatly accelerated by convection currents in the liquid. Such currents, which result in more rapid mixing, are known to occur visibly in many living cells (protoplasmic streaming) and they probably occur commonly in water-filled spaces throughout the plant body.

When water particles migrate by diffusion each particle moves on its own, as it were, like the particles of a solute. When

water moves by mass streaming it carries with it its dissolved particles—the solution flows as such—but mass flow through a colloid layer that retards some of the solute particles may leave those particles behind, the layer acting like an osmotic filter. It therefore follows that, for a given difference in hydrostatic pressure between two regions of the plant body, mass streaming, or molar flow, can occur at a given rate only if the pressure difference is great enough to overcome the resistances that lie in the path of movement. With great pressure differences water may move rapidly through paths where diffusion itself might be more rapid than flow if the hydrostatic-pressure difference were not so great. The rate of flow is dependent on the magnitude of the pressure difference and on the amount of resistance encountered in the path of movement. There appears to be no doubt that both flow of water and solution and diffusion of water and solutes occur continually in the plant, tending always to equalize hydrostatic and osmotic differences between different regions, but always hindred by walls and protoplasm.

WATER USE AND WATER LOSS

The mention of hydrostatic gradients leads to the query: how do any regions come to have lower hydrostatic pressures than the tissues of the thoroughly soaked seed or than the absorbing walls of the root system when submerged? In the first place, we have seen that enlargement occurs because of the formation or accumulation of imbibing and osmotically active substances and structures in the enlarging tissues. These become relatively drier because non-water materials continually increase in them. They consequently receive water from the other regions, eventually from the saturated regions of the roots and the solution beyond. Water taken into enlarging cells may be called *growth water*. For rapidly enlarging tissues it must be supplied at a considerable rate.

We have also seen that water is used up chemically in the living cells; it is combined with carbon dioxide in illuminated green leaves, it is combined with the component atomic groups of substances undergoing hydrolytic splitting (as when starch and water produce glucose under the influence of enzym catalysis). Water so used may be called *metabolic water*. The rate of water supply required for metabolic processes is perhaps generally lower than that required for enlargement. But, as has been seen, metabolic processes involving water in chemical ways occur also in the reverse direction; respiration produces water and the reverse of hydrolytic splittings does the same (as when glucose polymerizes to form starch and water).

Solution is sometimes excreted or secreted from living tissues by gland action, the colloid chemistry of which is not yet well understood. Water leaving the plant in this way may be called *secretion water*. The rate of such secretion is probably sometimes as great as the rate at which growth water is used. Guttation and nectary secretion are examples of this process in healthy plants. A similar process, called "bleeding," is especially pronounced in the case of tissues wounded mechanically or by fungi, etc., in some plant forms. It may be temporarily caused by decrease in the resistance to internal hydrostatic pressure, as when walls are ruptured or digested.

Guttation, which is superficially analogous to perspiration and the secretion of water on the surfaces of mucous membranes in the human body, may be readily observed at the leaf tips of young grass plants such as wheat and oat seedlings, also at the margins of leaves such as those

of the garden nasturtium (*Tropaeolum*), Fuchsia, etc. The very dilute solution forms droplets and drips off or runs down on the outside. Guttation occurs generally only when the water supply to these tissues is very high and the rate of water loss or use in other ways is very low. A secretion very similar to guttation occurs sometimes in the interior of the plant body, where solution is forced from living cells into intercellular spaces or into dead cells. Spaces or chambers usually gas-filled may thus become partly or entirely filled with liquid. When this occurs in leaves we say they are injected, but many cases of injection occur by the inward flow of water through stomata during periods when the external leaf surface is covered with superficial water. Excretion of solution from cell vacuoles into neighboring intercellular spaces is apparently the immediate cause of the local and rapid decrease or disappearance of turgor in special tissues that exhibit quick mechanical movements, as in sensitive stamens (barberry), sensitive leaves (*Mimosa*), etc. Sap pressure, root pressure, etc., when they occur in uninjured tissues, may be closely related to this sort of active secretion. I shall revert to sap pressure farther on. Wound excretion is illustrated in the Mexican century plants ("mescal"), from the extruding liquid of which fermented and distilled beverages are prepared. It is also seen in the coconut and other tropical palms, which supply similar juices that are used in similar ways.

Nectaries are common on floral parts and leaves of many plants. From floral nectaries the amount of excretion of water is generally comparatively slight, but foliar nectaries sometimes behave much like guttation glands.

After all these things have been considered, however, the most important water requirement of most ordinary plants, and of our experimental plant with its roots in solution and its foliage in the air of an ordinary room or greenhouse, is the requirement of *transpiration water*. The superficial walls of leaves and stem are exposed, unlike those of the roots in their usual environment of moist soil, to the atmospheric gases; they are not generally covered by liquid water. At these surfaces the water mass of the plant distinctly terminates, and each water-plugged ultra-microscopic pore, where its outer opening is in contact with gas, has a tiny water-air meniscus. It is through these menisci at the outer openings of colloid pores that the water of our plant is in direct contact with the surrounding atmosphere, as we have seen. When intercellular gas-filled spaces are not at all injected their peripheries present the same picture. The pores and their menisci may be less frequent and smaller (cuticle) or more frequent and possibly larger (walls of intercellular spaces like those connecting with the stomatal openings). In the latter case the menisci may be continuous laterally with a very thin superficial film of liquid that bridges the intervals between the pores. There is always such a film of adsorbed water, but its comparative immobility renders it negligible, for it acts much like the solid material that holds it.

Now, wherever liquid water or aqueous solution is in contact with gas there must occur either vaporization or condensation. Speaking more carefully, both must occur but one is generally more rapid than the other. Since the air about the leaves of our plant is seldom saturated with water vapor to the point where condensation would surpass vaporization, it follows that there is generally considerable loss of water by evaporation from the exposed menisci. This is transpiration. Transpiration water does not

leave the plant as a liquid, it vaporizes as it leaves. Transpiration tends to dry the exposed walls, to make the menisci retreat deeper into the wall pores. But they do not generally retreat to any considerable extent, for new water moves continually into the drying walls from the interior of the plant, and consequently the outer walls do not really become more than incipiently dry. The rate of transpiration is generally high, much higher than that of all other water losses and water uses combined, and one of the main requirements for plant health is generally the necessary supply of water that replaces transpiration loss. This consideration is at the base of all agricultural irrigation.

Water must be supplied to the absorbing roots a little more rapidly than it is lost by transpiration, or else the water mass of the plant must shrink. If it shrinks the first notable effect is to reduce the turgor of living cells in some regions, which actually wilt if turgor pressure becomes zero. Enlargement cannot proceed without turgor, and growth ceases before wilting begins. But some parts of a plant (as the older leaves) may lose turgor, wilt, die, and dry up, while other parts (as growing tips) are still turgid and growing. This is partly because water movement through the tissues along some paths is so hindered by resistance that the drying cells may die and become filled with gas in spite of the fact that there is slow movement into them from other parts. The occurrence of wilting in some tissues before it occurs in others is also partly due to differences in turgor pressure.

It should be noted that the transpiration rate must become zero when evaporation from the air-exposed surfaces ceases, especially when the leaves are covered with a layer of liquid water, as in long rainy periods. Conditions that promote the formation of dew on leaf surfaces may bring transpiration almost or wholly to a standstill. At such times leaves and stems may absorb some water, just as do the roots in our experimental solution culture. But the possible rate of water absorption through leaf and stem surfaces is very low, for cuticle, cork walls, etc., contain but little water when fully saturated, and water movement through them is correspondingly slow for any pressure differences that occur.

Another observation of importance in some cases is this, that one portion of a plant may shrink and give up its water to other portions, although the cell walls remain at first impregnated with imbibition water. This suggests another internal source of water for growing tissues. Since the water here referred to is characteristically set free through the wilting of tissues we may term it *wilting water*. It is, in a sense, the reverse of growth water. In periods of great aridity, of high transpiration rates and low absorption rates, some parts of the plant may maintain health and growth partly or wholly at the expense of water previously held for a long time in the cells of other parts. A massive cactus plant may blossom and produce fruit annually for several years without any entrance of water from without. In the meantime the water-storage tissues shrink and eventually die, even the intervening cell walls being largely oxidized, thus adding some metabolic water to the wilting water removed. Transpiration continues slowly, and yet new growth occurs each year, in the production of blooms and even rather juicy fruits. Partly developed fruits of plants like the orange may be thus sacrificed in times of drought. Succulent plants like the live-forevers (*Sedum*, for example) may grow for weeks in a plant press unless the protoplasm has been killed by immersing the specimens in boiling water before placing them in press.

We may summarize the several forms of

water supply and water requirement as follows:

Water requirements	*Water supplies*
Growth water	Wilting water
Metabolic water	Metabolic water
Excretion water	Water absorbed through leaf surfaces, etc.
Transpiration water	Water absorbed through root systems.

For general purposes we may neglect all forms but the last in each category. The main water requirement of most ordinary plants is transpiration water, and the main supply comes through the absorbing surfaces of the root system. We shall now consider the general mechanics of root absorption and transpiration a little more closely.

WATER ENTRANCE THROUGH ROOTS

The root system of our experimental plant is in a nutrient solution, and the outer walls of roots and root hairs are in direct contact with the surrounding liquid. The water mass of the plant is therefore continuous through these walls with the solution on the outside. There is no external resistance to the entrance of water into these walls from without. We neglect the slight osmotic resistance due to solutes in the nutrient solution that are not able to pass into the walls as rapidly as water does; such resistance is negligible when the nutrient solution is sufficiently dilute (when its osmotic value is of an order of magnitude of 0.1 atmosphere or lower). The rate of entrance of water through the roots of our plant must consequently be determined by conditions effective within the body; the weak solution can supply water to absorbing root surfaces as rapidly as absorption may occur, even though some of the solute particles of the medium may be shut out by osmotic or electric conditions. The water-supplying power of such a liquid medium is practically without limit, so long as the medium bathes the absorbing surfaces.

TRACTION IN LIQUID WATER

It was said above that one particular physical principle has recently come to appear fundamental in our conception of plant water relations. I referred to the capacity of water, aqueous solutions, and other liquids to transmit traction. This property of liquids has long been known, but it is generally neglected in treatises where one might logically expect to find it discussed. Most physicists and plant physiologists now appear to have but a vague appreciation of this characteristic of water. We may here consider it briefly from the physical point of view and then turn to its importance in plant physiology.

Water, mercury, and other liquids exhibit a high degree of cohesion but a low degree of viscosity, as compared with solids; we suppose that their particles are strongly attracted to one another but move upon one another with but very little resistance. It is therefore easy for some minds that have not become thoroughly familiar with the experimental and theoretical evidence, to regard the transmission of traction through a mass of liquid as no more than a myth. But the tensile strength of liquid water and weak aqueous solutions amounts to at least several hundred atmospheres. This may be deduced from other characteristics of water, and the phenomenon of taut water may be readily demonstrated experimentally.

The demonstration may conveniently follow the method of Berthelot or that of Böhm and Askenasy. In both cases a rigid wall is provided for the experimental water mass, of glass, porous porcelain, wood, etc., and precautions are taken to

insure at the outset thorough adhesion between the wall and the liquid. Gas bubbles of considerable size must be avoided, but dissolved air in the water does not hinder successful demonstration.

By the Berthelot method, much improved in detail by Dixon, a closed glass tube some 30 cm. long and nearly filled with water is carefully heated till the water expands and completely fills the cavity, while the originally enclosed air goes into solution. The whole is then cooled. The liquid tends to contract on cooling, but it adheres so strongly to the glass walls and its cohesion is so great that it remains filling the tube completely at a much reduced temperature. Under these conditions the water mass is actually stretched, which demonstrates the presence of traction strain. Dixon reports an experiment in which a mass of water at 72.9°C. occupied the volume natural to it at 84.9°C., a stretching amounting to 158.4 atmospheres of pressure. The hydrostatic pressure in the stretched water is negative and numerically equivalent to the stretching strain. The liquid is greatly supersaturated with air, and yet no bubbles form. The water mass finally ruptures as the temperature is lowered, when a pronounced click is audible.

By the method of Böhm and Askenasy the demonstration is even more striking, though the magnitude of the strain produced by this procedure is thus far only of the order of an atmosphere or two. Böhm employed a cut twig of arborvitae suitably joined to the upper end of a vertical glass tube filled with water. The lower end of the tube dipped into mercury below. Transpiration from the leaves caused the mercury to rise to a height of about 90 cm. above the mercury level in the reservoir. Since the atmospheric pressure on the reservoir meniscus (equivalent to somewhat less than 76 cm. of mercury column) could not support the liquid in the tube to such a height, it is clear that the water in the twig and in the tube, as well as the mercury in the upper portion of the latter, were actually supported by a pull from above, not by a push from below. Askenasy's classical experiment is like Böhm's, but Askenasy used a funnel filled with solidified plaster of Paris instead of Böhm's twig. In the hands of later workers the funnel and plaster are replaced by a porous porcelain plate or bougie suitably attached to the tube, as by means of a rubber stopper. A modification of this experiment, with special procedures that make success with it almost certain, has been recently described in the third American edition of Palladin's Plant Physiology, and a succinct account of the main aspects of the physics involved has been given by Livingston and Lubin in *Science* for April 15, 1927.

The pores of the porcelain are plugged with water, and the air-water meniscus at the outer opening of each pore is held fixed by capillary forces resulting in an imbibition pressure capable of withstanding an excess of several atmospheres of external air pressure. It is these pore menisci that prevent the entrance of air, just as in the case of the pore menisci of the outer walls of the leaves of Böhm's twig. Undissolved air cannot enter the system until one or more of the water plugs have been forced inward through the wall. But water evaporates from the pore menisci, as in the case of the external walls of plant leaves, and the hydrostatic pressure within the bougie and tube is consequently decreased. The water column shortens as evaporation proceeds, and mercury rises in the tube from below, replacing the water lost above. The hydrostatic pressure at the mercury-water boundary decreases progressively

as the boundary ascends, becoming zero when the column of mercury just balances the opposed external pressure due to the atmosphere acting on the mercury-air surface in the reservoir. At this time the pressure at every level in the mercury is positive, being greatest at the bottom and zero at the top of the column, and the pressure at every level in the water is negative, the negative value being greatest at the top of the system and zero at the mercury-water boundary. With the continuation of evaporation from the bougie and the consequent farther ascent of the mercury-water boundary, the pressure in the upper portion of the mercury also becomes negative.

By the Askenasy method it is possible to demonstrate an atmosphere or more of negative pressure at the top of the system before the column ruptures. (Why it ruptures in this experiment is not understood. Nothing approaching the tensile capacity of water or mercury has yet been shown in this way, but this method is more suitable to demonstrate the principles involved than is the Berthelot method, although that gives very much greater strains.)

The liquid having negative pressure is really slightly stretched, as in the Berthelot experiment. The water adheres to bougie wall, stopper, tube, and mercury, and the whole upper portion of the liquid mass hangs on the practically rigid walls just as the water mass of Böhm's twig does when negative pressure has been developed by transpiration. The negative pressure is an inward pull on all walls.

One further consideration in regard to the Askenasy experiment requires special attention. In the earlier stages, before negative pressure has appeared at all, the ascent of mercury in the tube is of course due to the pressure difference between the outside and inside of the system, but both pressures are positive and the difference is positive. In these earlier stages the experiment demonstrates suction but not tension in the liquid. As every one knows, the limit of suction is the current atmospheric pressure, as shown by a barometer. The continued rise of the mercury column beyond the height representing the magnitude of the current atmospheric pressure *appears* to show the development of a sort of super-suction, but the word suction should not be employed where traction is meant. In suction the moving liquid is affected by two opposed but unequal pressures, both tending to compress the liquid. In traction also there are two opposed and unequal pressures, but both tend to overcome the cohesion of the liquid and thus stretch it. In suction the liquid is *pushed* up; in traction it is *pulled* up. In suction the enclosing walls are pushed inward by positive pressure of the atmosphere; in traction they are not only thus pushed inward but also pulled inward by the negative pressure in the liquid. In these experiments traction does not begin to be manifest until the possibilities of suction have been surpassed.

PRESSURES IN THE PLANT

Turning once more to our experimental plant, with its roots in aqueous solution and its stem and leaves in air, and keeping the Askenasy experiment in mind, we readily appreciate why the water lost by transpiration, etc., or used in growth or metabolism, is generally replaced by water entering through the root surfaces. The whole plant corresponds to the bougie and tube of the Askenasy apparatus, but it is water that enters below instead of mercury. As transpiration water leaves the foliar surfaces, to use the most striking example of water use or loss, the hydrostatic pressure within the plant is cor-

respondingly reduced, and water movement occurs from the root surfaces to the leaf surfaces, mainly along the paths of least resistance; that is, through the vessels, which extend from root to leaf. The upward stream flows around enclosed gas-filled spaces and regions of too great resistance, but the strain tends always to extend throughout the entire water mass and in all directions. The gas masses of enclosed spaces expand as much as possible, but their expansion is checked by their surrounding water-plugged walls. This applies to gas-filled vessel segments as well as to intercellular spaces and ordinary cells that contain undissolved gas. The gas pressure in such spaces is low, but it is of course positive in sign; considerable negative pressures do not occur in gases under ordinary conditions.

If our plant is only a few centimeters high and if the transpiration rate is not too rapid, entrance and movement of water may be wholly accounted for by suction, but with higher rates of water loss suction alone can not make good the deficiency, and negative pressures are then developed in the water mass of the plant. If the plant is tall enough to have its water mass higher than the water-barometer column (about 10 meters), negative hydrostatic pressure and liquid strain must have been developed in its upper portion by growth alone, without considering rates of upward movement of water or resistances at all. It is very doubtful whether ordinary plants, even very small ones, could develop or exist in natural environments if it were not for the capacity of water to transmit traction pressure of many atmospheres when held in the colloid-osmotic structure typical of all plant bodies.

If the plant is of low stature, if the transpiration rate is low enough, and if the roots are covered with liquid water, traction will not occur. This case corresponds to the earlier stages of the Askenasy experiment. The inwardly directed, positive pressure exerted on the periphery of the plant body by the atmosphere tends to move the outer walls inward, to overcome the turgor pressure of superficial cells everywhere (thus tending to cause their collapse and the extrusion of their contents), to compress all cell walls, imbibition water, and the whole water mass of the plant, and to decrease the volume (and increase the gas pressure) of all enclosed gas-filled spaces. This is opposed by the turgor pressure of the outer living cells and by the resistance of the liquid and of the cell walls to compression. When some water is removed from the mass at any point (as by growth, metabolism, transpiration, etc.), the internal hydrostatic pressure is decreased and the plant body tends to shrink, but water enters through the roots and makes good the loss. Without the development of liquid strain (hydrostatic pressure of negative sign), however, the difference between the general internal pressure and the external pressure can never exceed about one atmosphere; for the internal pressure cannot thus be lower than zero and the external pressure does not exceed about one atmosphere under natural conditions.

If, however, the plant is taller than the suction column of water, or, even when it is of low stature, if the transpiration rate is sufficiently high in relation to the rate of water absorption by the roots and that of conduction to the leaves, then liquid strain occurs in at least portions of the water mass. Since water adheres very firmly to the peripheral walls, this negative pressure is numerically added to the atmospheric pressure; the inward pull is added to the inward push.

The turgor pressure (largely osmotic)

of the cells needs special attention. This tends to keep the cell walls stretched sufficiently so that their elasticity results, for each cell, in an inwardly-directed pressure equivalent to the turgor pressure. Each turgid cell occupies as much space in the water mass as the elasticity pressure of its stretched walls permits. Turgor pressure is generally of a magnitude between about 3 and about 15 atmospheres, but it is greater than 100 atmospheres in some leaves, etc., of plants grown in arid habitats.

Excepting at the periphery of the plant and at the periphery of gas-filled spaces, however, turgor pressure is without direct influence on the general hydrostatic pressure of the water mass, for it is opposed and equalled, for each turgid cell, by the elasticity pressure of the wall. Consequently it is local. In the interior of the water mass, a turgid cell is not unlike a closed rubber bag distended by water that has previously been forced into it, the bag being completely submerged in a large tank of water. The hydrostatic pressure of the tank is clearly independent of the turgor of the bag. Although fluctuations in turgor pressure in interior cells are without influence on the general hydrostatic pressure, still they must tend to produce shiftings of the wall positions, just as the wall of our rubber bag would change its form and position in the tank if we were to force more water from the tank into the bag or let some of the contained water out of the bag into the surrounding liquid mass.

For peripheral cells the relations are very different, since water may here escape from or enter the entire system, but undissolved gas cannot enter. If water is removed from such a cell, and not replaced, its flexible outer wall moves inward, the volume of the general water mass being correspondingly decreased. The inner walls move outward a little also and there may be many slight shiftings of walls in the plant interior. If water removal continues sufficiently long, without corresponding replacement, these cells collapse, turgor having disappeared. To bring this about with nothing but positive pressures it would of course be necessary that the environmental pressure should be greater than the local turgor pressure. This rarely if ever occurs, but internal traction is added to the environmental pressure. The removal of water from the plant at any place, within or at the periphery, decreases the volume of the general water mass and results in shrinking or wilting of peripheral cells unless water enters the body in equivalent volume. It is to be noted that the category of peripheral cells includes all living cells abutting on internal gas-filled chambers, as well as those under the direct influence of the outer air pressure.

Hydrostatic pressure, whether positive or negative in sign, is transmitted equally in all directions throughout the liquid mass, and water movement between peripheral cells and the rest of the system tends to equalize differences of pressure, as has been seen. Thus some peripheral cells wilt, collapse, and die, while others, because of higher turgor pressure or greater resistance to collapse on account of wall strength, may maintain their volumes. Leaves may wilt while growing points are still enlarging, etc. Transpiration from leaves tends to produce wilting not only in leaves but also in all peripheral cells, as in root hairs not externally in contact with water that may enter under the influence of a pressure less than their turgor pressure.

In the case of gland action solution may, as we have seen, be pressed out of the cells, traversing the cell walls. It may (*a*) pass to the outside of the plant, (*b*) pass

into a previously gas-filled space, or (*c*) simply pass into the general water mass of the plant, in which case the result is merely a shifting of cell walls. Gland cells must, however, derive their secretion water from the general water mass or else from the outside, through externally wet peripheral surfaces. If water is adequately supplied through the roots a gas-filled space may become filled with liquid, or solution may be actually extruded from the plant, without necessitating any shrinkage of the water mass or collapse of any peripheral cells. But without adequate water supply such liquid movement must have the same general results as that produced by transpiration.

Like osmotic pressure in individual cells, gland action in the interior of the water mass may result in the local development of hydrostatic pressure higher or lower than that of the system in general, but, as has been said, such local pressures must be without influence on the hydrostatic pressure of the water mass in general, as related to the exterior. Local internal secretion has been made much of by many writers on the movement of water in plants, but hypotheses that involve secretion as an essential feature of the general movement all fall to the ground when subjected to physical analysis with due regard to the pressure and energy relations and to all the facts that are known. There is no doubt that slow local movements from place to place in the plant may in many cases be referred to active secretion, just as guttation and the excretion of nectar are so referred, but the general flow of water from roots to leaves appears to be explained without any direct reference to such so-called vital action. (It is highly probable that the phenomena of secretion or excretion may soon be explained by reference to colloidal and osmotic phenomena, but this is not the place to attempt any analysis of the possibilities of the case. To mention the phenomena of coagulation, alteration in pore size, syneresis, may be suggestive. When the physics of secretion becomes better understood that advance will surely remove another prop from vitalistic thinking.)

Consider now the hydrostatic pressure just within or behind the water-air menisci that close the pores in an exposed, water-impregnated wall of a turgid cell, such as the wall of a substomatal space. The pressure of the atmosphere is not sufficient to force the liquid plugs from these water-plugged pores and therefore undissolved air cannot enter. The external walls are supported by turgor pressure. Removal of water by transpiration, etc., results in a pressure at the point in question lower than that exerted on the external water in contact with the absorbing root surfaces. It is the difference between these two pressures that produces inward or upward flow. If the smaller, inner pressure is positive the difference, as we have seen, cannot significantly exceed one atmosphere. If the inner pressure is negative (the liquid being then in a state of strain) the difference may amount to many atmospheres, depending on the negative magnitude. In general, the atmospheric pressure on the exposed walls, plus any traction that may be present in the water mass, results in a pressure tending toward collapse of peripheral cells and enlargement of the gas spaces. This outer push and inner pull tend to reduce the volume of all water-filled parts. But to the resultant pressure is opposed the rigidity of the colloid and osmotic system. This rigidity is partly due to the ordinary mechanical strength of cell walls, but in active tissues (with thin walls) it is due mainly to turgor. It is the turgor of the leaf

parenchyma alone that prevents the collapse of these cells. A peripheral cell can maintain turgor only so long as its actual osmotic and imbibition pressure is greater than the sum of atmospheric pressure and whatever traction exists in the water mass of which these cell contents are the outer part. If the turgor pressure is surpassed these cells collapse and the leaf wilts. If the pressure difference continues to increase, air finally finds its way into cells, vessels, etc., the water plugs in the larger pores of the walls being the first to give way unless the collapsing walls are actually torn open. Such cells play no further part in the water mechanics of the system, excepting that they act to retard water loss from the deeper, still living cells.

We thus see that turgor pressure in thin-walled cells is highly important in maintaining the water mass of the plant without too great decrease in volume or other alteration in form that would destroy it as a mechanism. It used to be thought that osmotic attraction might somehow play an important and immediate part in the entrance of the water stream through root surfaces and in the flow of the transpiration stream, but hypotheses on that basis must be laid aside, although they are still commonly presented in vague and unsatisfactory ways in text books of plant physiology. Osmotic pressure of peripheral cells is of fundamental importance, but not directly; it practically sets a limit to the magnitude of the motivating pressure difference (mostly traction) that can develop in a plant.

What has been said about leaf parenchyma applies also, *mutatis mutandis*, to all thin-walled living cells throughout the plant body. Turgor pressure, whether due to osmotic pressure or to imbibition pressure, tends to maintain the form of the living cells in the body; that is, it tends to maintain the relative positions of the walls. It is essential to enlargement. The maintenance of turgor and form in living cells is doubtless generally essential to their metabolism as well as to the rigidity of peripheral tissues.

Special attention needs also to be given to the pressure relations of enclosed gas-filled spaces in the plant body. These were all originally parts of the liquid continuum, but their liquid contents have disappeared. Suppose an intercellular space nearly filled with water but containing a small gas bubble; where gas has come out of solution or where the taut water has been torn apart, for example. The bubble expands till its gas pressure and surface tension combined are just balanced by the hydrostatic-pressure difference between the surface and the interior of the water system in general, provided that this difference is not greater than the gas pressure and surface tension of the bubble when fully expanded so as to occupy the entire intercellular space. Such gas pressures in enclosed spaces can never be below zero, though they may rise to much above a single atmosphere when such a gas as carbon dioxide is actively discharged into these spaces from the surrounding liquid surfaces. Before the surrounding liquid becomes stretched (negative pressure) all free liquid has left the spaces, and their walls are like the outer ones of peripheral cells exposed to the atmosphere. These walls are then pulled outward, as has been seen.

As the longitudinal rows of cells forming the vessels mature many of the cross walls get dissolved and the protoplasm disappears, but the resulting tubes remain filled with liquid, and this transmits hydrostatic pressure in all directions. If a gas bubble of considerable size forms in a vessel segment, as by rupture of the

stretched water, it expands till that segment is completely filled with gas. Here again the taut water pulls the walls outward because it adheres in the pores. In some forms some of the vessels continue filled with water for years while the lumina of other vessels may be removed from the liquid system after a much shorter time. Many of the older vessels of the trunk of an old tree are thus gas-filled. Indeed, the whole interior of the trunk may decay while the tree remains healthy as a whole.

Water moves about the plant in all directions, in accord with hydrostatic-pressure gradients, always flowing most rapidly along paths of least resistance, as we have seen. Water removal is mainly at the top and water entrance at the bottom; consequently the most rapid movement is, in general, upward from root to leaf. Although lateral flow of water from one vessel to another at the same level generally encounters greater resistance per unit of distance traversed than does upward flow (for more walls must be passed, and often, also, the water masses of living cells), yet lateral movement occurs commonly enough to allow the stretched water to flow upward around the gas-filled segments in conducting bundles. Movement occurs wherever traction is developed, but it is slow or rapid, for a given amount of traction, according to the resistance encountered.

Old vessels that have become gas-filled do not generally become again filled with liquid, it seems, excepting possibly in plants of very low stature. New vessels are continually forming in the youngest regions of the tree trunk, however, and the number of water-transmitting vessels increases as the tree increases its diameter, in spite of the continual loss of transmitting vessels in the older parts of the xylem. We may say that the taut water strands of the vessels "wear out." It appears that they are not generally rejuvenated but that their rôle is taken over by newly formed ones.

It still remains an open question, however, whether gas-filled vessel segments in a conducting bundle may not sometimes become once more filled with water. If this occurs in the upper parts of tall trees it must be due to some special gland action of living cells. It is conceivable that sap pressure may sometimes inject liquid into a segment previously emptied of all but gas, at a rate rapid enough to result in bringing that segment back into the water system of the plant. This point requires further study, but all features of the rise of water in plants are generally cared for if we make the supposition that no vessel segment that has once lost its liquid is ever refilled. In other words, we may tentatively suppose that if the taut water mass is ever broken in a vessel segment it is never replaced, that segment remaining a gas space, an island in the water mass.

ROOTS IN SOIL

We may now examine the results of a complete cessation of water entrance through the roots, for which purpose we may imagine that we have transferred the root system of our plant to water-saturated air. We suppose that the leaves are still exposed to ordinary air and that transpiration continues. The film of solution adhering to the roots is soon absorbed, and ultra-microscopic air-water menisci are then formed at the outer openings of the pores of the peripheral root walls, just as in the case of walls bounding substomatal spaces in the leaf. The water mass of the plant is now completely bounded by water-plugged walls and is in contact with gas at the outer surfaces of these walls. But the periph-

eral water menisci are so strongly held in the wall pores by adhesion and surface tension that it would require many atmospheres of gas pressure to force them inward. However, as we have seen, outside of laboratory procedures the gas pressure is never greater than about one atmosphere.

Since the roots of our plant are bathed in water-saturated air we may assume that no evaporation occurs from their surfaces, but neither can water enter (unless possibly a negligibly small amount of condensation may occur). (If the air about the roots were unsaturated transpiration would occur from the root surfaces as well as from the aerial parts.) Transpiration from the leaves continues to reduce the volume of the water mass, and the inner pressure decreases gradually; that is, being negative in sign, its numerical value increases. Eventually the inward traction becomes greater than the turgor pressure of peripheral living cells, the latter decreases to zero, and wilting occurs. The first cells to wilt may be those most exposed to evaporation in the leaves, but the traction in the liquid mass of the plant being transmitted in all directions, the root hairs and other superficial cells of the roots very quickly come to the same condition; wilting of delicate roots, under our experimental conditions, occurs almost as soon as wilting of leaves. It should be added that tissues with exceptionally high turgor (due perhaps to a large sugar content and a resulting high osmotic pressure) should resist wilting when the tension in the general water mass is sufficient to produce the collapse of cells with lower turgor pressure. It thus comes about that not all parts of a plant show the onset of wilting at the same time or with the same negative pressure in the vessels, etc. If a high transpiration rate is maintained (as with leaves exposed to sun, warm air, and wind) most of the outer peripheral tissues of the plant, including all the younger roots as well as the leaves, eventually wilt, break their water continuity with the remaining parts, and dry up.

Let us next consider the condition of roots in an ordinary soil, containing a considerable amount of water (soil solution). The young roots and root hairs growing into new regions are at first surrounded by at least thin layers of solution, and absorption goes on as though the roots were in free liquid. Water is of course required for root enlargement, and some of the water taken up may therefore be fixed in the new root tissue. It seems probable that roots may sometimes push considerable distances into a region of the soil that does not supply enough water for even this growth, the soil-water films being too thin; in such cases the growth water of the advancing roots must be drawn from other roots, which may be in wetter regions, or perhaps from water previously stored in other parts of the plant body. Such roots might be growing in the soil air, which is generally saturated or nearly saturated with water vapor.

With wet soils absorption of liquid water may continue for some time, but it eventually ceases unless water is added to the earth about the roots, as by rain, subterranean flow, or irrigation. Water moves but slowly through soils that are not very wet, and it now appears that root surfaces do not draw water from any great distances in the soil. They nearly dry the layer adjacent to them, and they continually advance into unexplored regions.

The outer cells of the roots of many kinds of plants grow out to form root hairs, which apparently occupy very thoroughly a cylinder of soil around the root, to a distance of a centimeter or so.

Root hairs are short lived; apparently their collapse and death are in many cases brought about by internal traction when the adjacent soil-water films are depleted and absorption ceases. They are very delicate, very thin walled, and they do not generally last long in any event. There seems to be no doubt that root hairs, when present, act as absorbing surfaces, but they are not essential, for many plants grow well without them and many forms never produce them.

The zone of root hairs, a little behind the root tip, proceeds forward with the advance of the tip itself, and, in merely moist soils, the soil films with which contact is made give up most of their water. If this be a true picture, a plant rooted in a not very wet soil would soon succumb to inadequate water supply if root enlargement were to cease. It seems that numerous fine rootlets and their branches, often provided with root hairs for a period, are continually sewing the soil mass through and through, picking up soil solution as they come to it, somewhat as a vacuum cleaner picks up dust. Before root growth is completely checked most of the water originally present has been absorbed from the whole soil region through which the root system has been operating, provided of course that all other conditions that influence root growth and absorption of water are adequate.

SOME MAGNITUDES AND RATE RELATIONS

As to the magnitudes involved in the phenomena we have been considering, the turgor pressure of living cells in ordinary plants amounts to, say, from 1 or 2 to 12 or 15 atmospheres. In the leaves of desert plants it may exceed 100 atmospheres. Imbibition pressure appears to be low usually, except perhaps in embryonic tissue, resting seeds, etc. When the imbibing material is nearly saturated with water, as in cell walls generally throughout the plant body, the actual pressure exerted by the tendency to swell is of course approximately balanced by the turgor pressure of the cells and may be estimated as usually amounting to from 1 to 15 atmospheres in turgid tissues. The less nearly saturated the imbibing material, the greater the swelling pressure developed by the imbibition of an additional increment of water. Dry starch attracts the first increments of imbibition water with a pressure of over 2500 atmospheres. A gelatin gel containing 28 g. of gelatin to 100 g. of water attracts additional water with a pressure of about 200 atmospheres. Ordinary porous porcelain, such as is used for filters, atmometers, etc., or for the Askenasy experiment, holds imbibed water against a gas-pressure gradient of from 1 to 5 or 6 atmospheres. (Of course such material does not alter its volume with change in its water content, and its structure is different from that of cell walls and protoplasm.) The exposed cell walls of xerophytic leaves hold their water of imbibition against pressure gradients of 100 atmospheres or more.

In the dry seed imbibition attraction appears to be very great. The first swelling of a seed may, in many cases, be largely due to imbibition pressure and the swelling pressure amounts to many atmospheres. The negative hydrostatic pressure (strain or traction) in the vessels of plants of low stature frequently attains a magnitude as great as that of the turgor pressure in the leaves, for it is common to see the foliage of such plants wilted in the middle of the day. Renner concluded, from some ingenious measurements, that the liquid strain in stems of low shrubs such as Forsythia was between 1 and 5 atmospheres. The tran-

spiration rate was low, and the soil about the roots was very wet at the time. In the tallest trees the strain near the top must be at least of the order of 10 or 12 atmospheres.

Water frequently moves upward in the xylem of plants at a rate of 30 cm. per hour or at still greater rates. Transpiration occurs from leaves at rates up to a few hundredths of a gram per hour per square centimeter of foliar surface. Root tips generally advance through the soil at rates of a few centimeters per day. Soils in which plants are beginning to wilt can generally supply less than 10 mg. of water per square centimeter of absorbing surface for the first hour of contact.

In ordinary healthy plants the rate of water absorption through the roots is about equal to the rate of transpiration; the absorption rate is a little greater by night than the rate of water loss and a little smaller by day. The transpiration rate itself is generally much greater by day than by night. As long as the soil can supply an adequate amount of water to the advancing root system the rate of absorption is determined by the transpiration rate and internal conditions, but when the supplying power of the soil is inadequate that becomes the limiting condition.

The transpiration rate is of course determined largely by the extent of the leaf surface, as well as by the nature of the peripheral walls, stomatal arrangement, leaf shape, etc. Fluctuations in the rate per unit of leaf surface in any plant are dependent mainly upon air conditions but also, in many forms, to a considerable extent upon changing size of the stomatal openings. This rate may be two or three times as great with open as with closed stomata. It is not unusual for the air conditions that influence the transpiration rate to have day values five or ten times as great as the night values. For example, if the rate of stomatal transpiration is taken as unity for a night period, with unity as the corresponding value of the evaporating power of the air, then the rate for a day period might be 3 if the evaporating power of the air remained at unity, but if this external influence had a day value of 5, the transpiration rate for the day period would be 15.

Rates of transpiration, and of absorption, may also be limited by the water-conducting power of the plant; the conducting system may be inadequate, even with wet soil. Wilting of diseased plants is often due to plugging of the vessels by parasitic fungi. It is sometimes supposed that the lowering of the vapor pressure of the water in peripheral cell vacuoles, due to the presence of dissolved substances, may be effective in retarding water loss by transpiration, but such retardation cannot be significant. Even if the vacuolar solution extended through the wall to the exposed surface, which it does not do, evaporation would be retarded less than ten per cent in the case of the most concentrated solutions ever recorded for plant vacuoles.

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MILK SECRETION AS INFLUENCED BY INHERITANCE

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MILK in general is a sex-limited product, as the secretory activity of the mammary glands is limited to females of the mammalia. The first product of milk secretion, colostrum, is striking in its composition and markedly different from that to follow. It is richer in the albumin and globulin fractions of the protein and in the salt. It contains many cells, frequently spoken of as milk corpuscles, which contain nuclear material. The fat has a higher melting point and contains more cholesterol and lecithin than the subsequent milk. Our scant present-day knowledge of this product shows that it is important in protecting the young of several species against immediate bacterial invasion. After a week or so from the time of parturition the mammary gland secretion loses the characteristic properties of colostrum and assumes those common to normal milk. As yet no data are available to investigate the relation which exists between colostrum and the secretion of a later period.

Considering the world in general, the milk used for human consumption may come from a number of different species of animals. Thus milk from cows, sheep, goats, mares, camels, etc., are all products used in the human bill-of-fare. Here in the United States almost the only source of milk and its products is the dairy cow. It is because of this fact that the available records on the amount and quality of milk are almost entirely limited to this species. The data, from which our information relative to the factors affecting milk production is obtained, are consequently confined almost entirely to dairy cattle.

Cow's milk is made up of protein, fat, sugar, and salts. The protein may vary from 2 to 5 per cent of the milk's weight; the fat from 2.0 to 8.0 per cent; the sugar from 3.5 to 7.0 per cent; and the ash from 0.63 to 0.84 per cent. The protein is largely composed of two substances, casein and lactalbumin. These substances are characteristic of milk and are, in fact, characteristic of the species giving the milk. Butterfat is also of characteristic composition, containing mainly the fatty acids, butyric, caproic, oleic, palmitic, and stearic. The sugar of milk is lactose, a product characteristic of mammary gland activity. The ash is composed of several salts, calcium and phosphorus being the predominant elements. Besides these major products there are many minor constituents of milk whose importance in the general economy of animal life is but now coming to be recognized. In other words, milk is a highly complex metabolic product.

MECHANISM OF MILK SYNTHESIS

The combined efforts of earlier investigators have given us hypotheses, imperfect though they are, to account for the mechanism by which the animal body supplies the raw material to the mammary

gland for the making of its products. As blood is the common carrier for most of the materials utilized in metabolism, it is natural to turn to it as the source of the precursors of the milk solids. The most fruitful method of analyzing what these precursors of the milk solids may be, has consequently been that of comparing the composition of the blood which is entering the mammary gland as contrasted with that coming away from it. This method of approach as first indicated by Kaufmann and Magne, in their hands and also that of Cary, has shown that the blood entering the mammary vein contains about 20 per cent more dextrose than that coming away from the mammary gland. Such being the case it is considered reasonable to suppose that the lactose, or milk sugar, is manufactured from the dextrose, or blood sugar. Meigs, Blatherwick, and Cary have utilized the same method to indicate the origin of the milk fat. They believe that the blood entering the udder carries more phosphatid than that leaving the udder; that the blood entering the udder carries less inorganic phosphate than that leaving the udder. From these two observations and the difference in the composition of milk compared to that of blood with regard to phosphorus, they draw the conclusion that the mammary gland in butterfat secretion takes phosphatid from the blood, converts it into fat, and returns as inorganic phosphorus the excess phosphorus derived from breaking down the phosphatid. Cary, following this same order of approach, shows that the blood entering the udder contains more amino nitrogen than the blood coming from the udder. From this fact and the recent work on the metabolism of protein he draws the conclusion that the proteins of milk are derived from the amino acids of the blood.

Another method of approaching this problem consists in the administration of some product which alters the composition of the blood or the general metabolism of the animal. Such a product, phloridzin, has been used frequently for this purpose. The results from its use, however, are complicated by the fact that it has broad physiological effects, not only causing a glycosuria but also markedly increasing the nitrogen elimination from the body. Another product which perhaps has more possibilities is insulin. In some preliminary experiments with this material Tobey and the writer found it possible to reduce the blood sugar of a lactating cow to three-fifths the normal. The milk of this cow was found to have slightly less lactose in it than it would normally have, roughly a reduction of 10 per cent in the total lactose. At the same time the ash showed a remarkable increase in its percentage. The other constituents were variable, varying in both directions around the normal. These results might tentatively be interpreted as supporting the conclusion that the dextrose of the blood is the precursor of lactose.

The problem before us may now be stated in physiological terms in the light of the foregoing facts. In studying milk secretion five large groups of metabolic products are dealt with: water, constituting roughly 87 per cent; sugar, 5 per cent; butterfat, 4 per cent; protein, 3 per cent; and ash, 0.75 per cent. Our present knowledge, scanty and irregular though it is, indicates that in the formation of these products the raw materials in the blood appear to be: dextrose, phosphatids, and amino acids. The problem in hand is to determine the influence of inheritance on controlling the variation in the metabolic activity of the mammary glands expressed as quantity and percentage content of the milk constituents.

Genetic studies largely limit themselves

to two major phases of this problem, the milk quantity, or the interaction of all of these variables to produce small or large yields of milk, and the butterfat percentage found in the milk. Besides these data there exists a small amount of information on the inheritance of the other milk constituents, as lactose, protein, and ash.

THE INHERITANCE OF MILK YIELD

The study of the inheritance of milk production is complicated by the fact that the metabolic activity of the mammary gland changes remarkably with the age of the animal. This change, as first noted by Pearl, is logarithmically related to the cow's age, or speaking in terms of lactation yield, the cow of two years of age gives a relatively small amount of milk. This yield is rapidly increased on the cow's second lactation at three years of age. The lactation yields continue to increase, but at an ever decreasing rate for each lactation, until the cow reaches her maximum production at between six to ten years of age. From this point the lactation yields tend to diminish at an ever increasing rate. Figure 1 shows graphically how this change of production takes place with increasing age for a herd of unselected purebred Jersey cows.

Figure 1 indicates the striking changes which take place in the metabolism of milk as the age of the cow increases. It further illustrates the attention which must be paid to these changes in comparing the production of cows whose lactations start at different ages. It is therefore necessary in all critical work on milk production to standardize the records to a given age or to utilize records which are made at a single age. Throughout this paper the writer has taken account of this factor age so that the conclusions are based on records standardized for age.

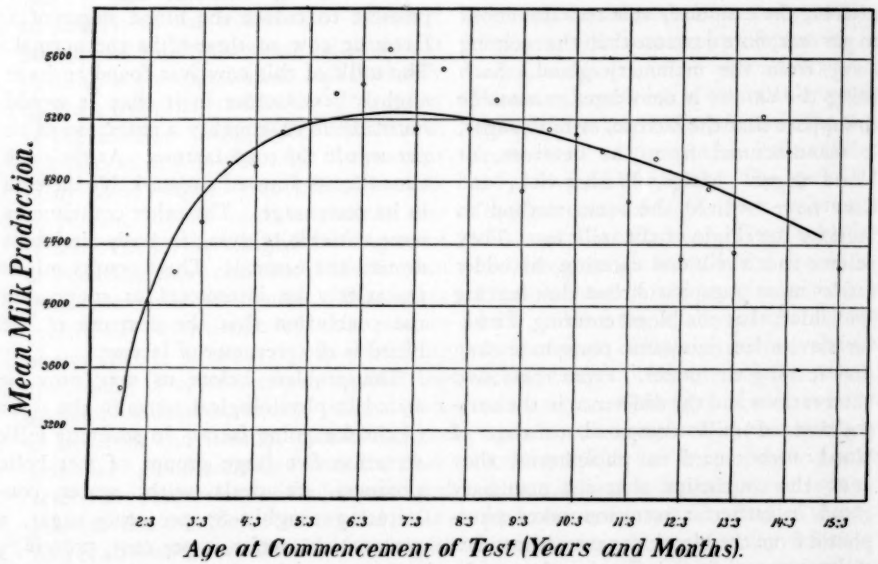

FIG. 1. DIAGRAM SHOWING THE OBSERVED MEANS (SMALL CIRCLES) AND THEORETICAL MEANS FOR JERSEY EIGHT-MONTH MILK PRODUCTION AT ANY GIVEN AGE

The record for the concentration of the different materials composing milk shows

less variation with age. Such being the case, age is not such an important factor in studying the concentration of any given item in milk as it is in studying the quantity of milk. This factor has, however, been taken into consideration, thus eliminating the extraneous influence of age on the concentration of the milk solids.

The general observation that milk yields differ between breeds has indicated that at the foundation many of these differences in producing ability are hereditary. But how and what are the limitations? It is plainly not a simple matter, for if it were, none of our cows would produce less than ten or twelve thousand pounds of milk a year. The problem is not so much to breed animals of higher production than any which we now have as it is to be able to reproduce the best of our present-day stock uniformly and at will. In other words, we wish to know what are the significant facts to be taken into consideration in breeding such stock and what items are of but trivial importance. This problem is made doubly difficult by the fact that it is impossible to measure the character of milk production in the sire. It is, in fact, only possible to arrive at a measure of the influence of the sire on the production of his daughters by indirect means. The first step to be taken towards the better understanding of this problem is, then, to find out the way in which the variations or differences in producing ability behave in their inheritance.

Two general methods of approach have been utilized. The first consists in making carefully controlled crosses between strains whose variation in milk production is known and which do not appreciably overlap in their producing ability. The second consists in studying the variation of production within a given strain of cattle and analyzing the influence of inheritance on this variation. This first method of approach has been utilized by Pearl, Cole, and in a practical sense by Bowlker (see Castle) and Count F. Ahlefeldt-Laurvig (see Ellinger). In a still more limited way the results of Parlour, Stevens, Kildee and McCandlish, Olsen and Biggar, and others, furnish data of some value when considered from this point of view. As the results of these different investigations appear to be alike in their conclusions, it seems necessary to review only the most critical of the work.

The experiment commenced by Pearl, and since 1917 carried on by the writer, consists of controlled matings of three groups of cattle. The first group, the Holstein-Friesian, represents high milk yield and low butterfat percentage; the second group, the Jersey and Guernsey, medium milk yield and high butterfat percentage; the third group, Aberdeen-Angus, low milk yield and a butterfat percentage nearly as high as the Jersey group. Besides these groups, the work also included a few Ayrshire animals with medium milk yield and a butterfat percentage intermediate between the Holstein-Friesian and Aberdeen-Angus. Thus in these classes there are strains of cattle capable of metabolizing large volumes of milk, strains capable of metabolizing medium volumes of milk, and those capable of metabolizing only small volumes of milk. Within these same groups there are strains which regulate this metabolic activity to produce small percentages of butterfat and strains which have high butterfat percentages. When the high milking group is crossed with the medium milking group, the milk yields of the resulting crossbreds are intermediate between the two, approaching most closely those of the high group. When the high milking group is crossed with the low milking group, the resulting crossbreds have milk yields intermediate between

the two, resembling closely that of the medium milking breed. The results appear to be essentially the same whichever way the cross is made. When the medium milk producers are crossed with the low producers, the offspring have milk yields intermediate between the two parental groups. From these results it is clear that it is possible to have an animal extremely heterozygous for its inheritance of milk yield and yet have its yield closely resemble that of a relatively pure strain. Furthermore, since the results are the same either way the cross is made, the experiment indicates the equal influence of both sire and dam on the milk production of the offspring. When the three groups of first generation crossbreds are contrasted it becomes clear, since none of these groups resemble each other or their immediate parents, that the inheritance of milk yield is of the blending type, probably dependent upon a number of factors.

This conclusion is confirmed by the results of the second generation backcrossed progeny. The milk production of these second generation cows shows but little evidence of clean-cut segregation. Production tends to be intermediate between that of the two strains crossed. The evidence thus points to the conclusion that the production of quantity of milk is dependent upon a number of different factors in its inheritance.

The production records of the first generation crossbreds between the high-producing Holstein-Friesian and medium-producing Guernsey group as made in the Bowlker herd have been analyzed by Castle. Thirty-one of these first generation heifers in their first lactation showed milk yields which resembled the Holstein-Friesian parent 1.9 times as closely as they did the Guernsey parent. In the second lactation the milk yield of these crossbred cows was 3.8 times as close to the Holstein-Friesian parent as it was to the Guernsey parent. These results, therefore, support those indicated above.

Ellinger has analyzed the results of the crosses between the Red Danish and Jersey cattle as made in Count Ahlefeldt-Laurvig's herd. Using ten weeks of the first lactation as his measure of the cows' producing ability and cows 28 to 35 months old, the Red Danish animals produced 1,975 pounds of milk, while the Jerseys produced 1,568 pounds of milk. The first generation crossbred animals produced 1,835 pounds of milk. The second generation Red Danish backcrosses produced 1,941 pounds of milk, whereas the second generation Jersey backcrosses produced 1,635 pounds of milk. For the third generation animals resulting from backcrosses of Jerseys onto second generation Jersey backcrosses, or seven-eighths Jerseys, the milk production was 1,543 pounds of milk. These results indicate that the inheritance is of a multiple factor type. The high milk yield shows that there is a tendency for the first generation crossbred's milk production to be increased slightly by heterosis, or that the factors for high milk yield are more dominant than those for low milk production.

BUTTERFAT PERCENTAGE

The influence of inheritance on the butterfat percentage of the crossbred cows for the experiments indicated above is of particular interest in that this influence finds expression in the regulatory processes governing the concentration of the solids in milk rather than those governing its quantity. It will be recalled that the information leads to the hypothesis that the phosphatids are the raw materials from which the butterfat of the milk is made. For Holstein-Friesian cows this butterfat ranges from 2.3 to 4.7 per cent. For Guernsey cattle the butterfat percentage

is much higher, ranging from 3.6 to 7.2 per cent. The butterfat percentage of Jersey cattle ranges from 3.3 to 8.0 per cent. The frequency distribution for Ayrshire cattle is still different, ranging from 2.5 to 6.6 per cent. Since the frequency curves for each breed's butterfat percentage are quite characteristic and distinct from those of the other breeds, it is evident that there is a distinct physiological mechanism by which a cow is able to concentrate butterfat in her milk. Such being the case, it is of interest to examine the results of crosses between these breeds as a means of indicating what part inheritance may play in controlling the cow's ability to concentrate this item of milk secretion.

The experimental matings forming the herd collected by Pearl and Gowen contain crosses of the four breeds, Jersey, Guernsey, Holstein-Friesian, and Ayrshire. The widest differences existed between the butterfat percentages of the Holstein-Friesian and the Channel Islands breeds, Guernsey and Jersey. Smaller differences were found for the Jersey and Ayrshire crosses. The results from these experiments show that the crossbreds from a high butterfat percentage group mated to a low butterfat percentage group have a butterfat percentage intermediate between the two groups but slightly nearer the low butterfat percentage group. The crosses of Ayrshire and Jersey give cattle whose butterfat percentage is also intermediate between the two groups. These results point to the conclusion that butterfat percentage is controlled in inheritance by multiple factors. Since there was no evident difference between those matings in which the sire and those in which the dam came from the high butterfat percentage group, it follows that the sire and dam appear to play an equal rôle in the butterfat percentage of their offspring. The second generation cows thus far obtained from this herd are largely backcrosses of the first generation animals on the purebred parents. These second generation offspring show a fairly wide variation in their butterfat percentages. There is but slight evidence of clean-cut segregation of the single factor type. The results clearly point to the deduction that the concentration of the butterfat in the cow's milk is dependent upon multiple factors.

The butterfat percentages of the crosses between the Holstein-Friesian and Guernsey cattle as made for the Bowlker herd and analyzed by Gaines and Yapp show that for 47 of these first generation heifers the butterfat percentage was intermediate between the two breeds. The variation of this butterfat percentage was rather large. For the second generation animals, the butterfat percentage was about the same as that for the first generation animals and the variation for the group was only slightly greater than that of the first generation. Here again the conclusions to be drawn from these data are the same as those indicated above,—that the sire and dam are equally responsible for the butterfat percentage of the cow and that this butterfat percentage is in large measure dependent upon a number of factors in its inheritance.

Ellinger's analysis of the inheritance of butterfat percentage by crosses between the Red Danish and the Jersey breed may be summarized as follows. The Red Danish breed is much like the Holstein-Friesian in that its butterfat percentage is low. For the cattle used as parents this percentage was 3.56 per cent. The Jerseys used as parents had an average butterfat percentage of 4.94 per cent. The first generation crossbreds were almost intermediate between the two breeds, namely, 4.21 per cent. When the first generation crossbreds were bred back to the Red

Danish breed, the butterfat percentage of these second generation offspring was reduced to 4.04 per cent. When the first generation crossbreds were bred back to the Jersey breed the butterfat percentage was raised toward the Jersey level, the average being 4.53 per cent. For these second generation backcross Jerseys bred back to a Jersey bull, the third generation offspring had a butterfat percentage of 4.60 per cent. These results show clearly the influence of both sire and dam on the butterfat percentage of the progeny. They likewise show that the butterfat percentage of a cow is dependent upon her ancestry, or that butterfat percentage is inherited and inherited in a typical multiple factor manner. These multiple factors may possibly show a slight tendency to dominance of the low butterfat percentage factors or heterosis may be effective in lowering slightly the butterfat percentage of the progeny.

INHERITANCE AS A FACTOR IN THE VARIATION OF THE OTHER MILK CONSTITUENTS

The metabolizing rates of Holstein-Friesian and Guernsey cattle differ with regard to their ability to synthesize the proteins of milk. Yapp has shown that for the milk of the Holstein-Friesians in his herd the protein content was 3.1 per cent, whereas for the milk of the Guernseys the protein content was 3.9. While this difference is not large it appears to be significant. The first generation offspring resulting from the cross of these two breeds have an average protein content of their milk of 3.4 per cent. In other words, the percentage of protein is intermediate between the two parental races. Little or no segregation is shown for the second generation offspring as their protein content was 3.5 per cent. From these results it appears that the animal's ancestry markedly influences the protein content of its milk and that the inheritance factors for this protein content show no clear-cut evidence of segregation.

The proteins of milk are probably synthesized from the amino acids of the blood. The results above quoted indicate that the ability to synthesize these proteins and to determine their concentration in milk is an innate factor within certain breeds. The results further demonstrate that the concentration of the proteins within this milk is an inherited characteristic of the animal wherein the parents play an equal part.

These same crosses are unsatisfactory as material to determine whether or not the lactose content of milk is dependent upon inheritance, for the Holstein-Friesian and Guernsey cattle used in these experiments had essentially the same lactose per cent. Thus the Holstein-Friesian breed's lactose per cent was 4.918 ± 0.041, while the Guernsey's lactose per cent was 5.100 ± 0.023. The lactose percentage in these two breeds must be determined largely by the same factors. The first generation crossbreds' lactose per cent was, however, intermediate between the two breeds, being 5.007. The second generation hybrid was also intermediate between the two breeds, being 4.989 per cent.

The results indicate that the ash of milk is an inherited characteristic similar to that of the other constituents. In the analysis no attempt was made to separate the different elements of the ash. The two breeds, Holstein-Friesian and Guernsey, differ by about 10 per cent in the ash content of their milk. The Holstein percentage is 0.68, whereas the Guernsey milk's content is 0.75 per cent. The first generation is intermediate with a tendency toward the Guernsey, its ash content being 0.73. The second generation is also intermediate between the two types with an ash content of 0.72 per cent.

There is no greater variability in F_1 or F_2 than in the parents, thus indicating that a number of factors are involved in the transmission of this composite character.

INHERITANCE OF MILK YIELD AND BUTTERFAT PERCENTAGE WITHIN PURE BREEDS

The variation of production or butterfat percentage within the pure breeds of cattle furnishes another group of data by which the mechanism controlling this variation may be further elucidated. As indicated above, milk production or butterfat percentage shows much less variation within the so-called "pure breeds" than in crosses made between breeds. The variation, however, is still large. Thus Holstein-Friesian milk production, in its Advanced Registry, varies between 9,000 and 35,000 pounds for the year period. The Guernsey milk production varies between 6,000 and 22,000 pounds for the 365-day period. The Jerseys show a similar range. The range of variation for butterfat percentage is also large for the pure breeds. The Holstein-Friesian butterfat percentage ranges from 2.3 to 4.7; that of the Guernsey and Jersey from about 3.5 to 8.0. The pure breeds plainly offer an excellent opportunity to test the influence of heredity on milk secretion.

The type of data found in the advanced registers of these three breeds necessitates a different analytical mode of approaching these problems from that heretofore utilized. In place of controlling certain variables, it becomes necessary to measure them and determine their effect within the given universe which permeates the data. The correlation method is suited to this purpose when, as in this case, the data conform in their behavior to the assumptions underlying it.

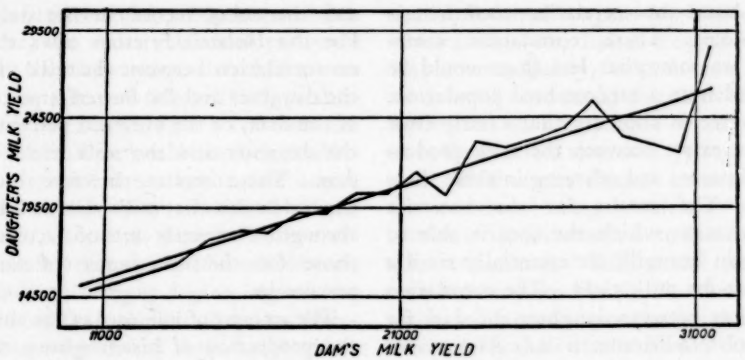

FIG. 2. RELATION BETWEEN THE MATURE-FORM PRODUCTION OF DAUGHTERS AND THEIR DAMS FOR HOLSTEIN-FRIESIAN ADVANCED REGISTRY CATTLE

The relation which exists between the milk productions of daughter and dam furnishes perhaps the most direct test of the effect of inheritance on this character. Figure 2 shows this relation between the milk production of daughters and dams in the Holstein-Friesian breed. The irregular line shows the actual average daughters' milk yields for the given dams' milk yields. The straight line shows the general trend of the data. From this figure it is clear that as the dams' milk productions increase, the daughters' average milk productions also increase. The increase is furthermore at a uniform rate. The

correlation coefficient measuring this relationship is 0.50 ± 0.02. It has been possible to show that this population is nearly random bred. Such being the case, and in view of the multiple factor nature of milk quantity inheritance, it would be expected that the correlation between the dam's production and that of her daughter would be 0.5. Thus the result of actually measuring this relationship checks exactly with that expected from previous knowledge and theory. The relation between the production of daughter and dam in the Guernsey breed is measured by a correlation coefficient of 0.36 ± 0.02. In the Jersey breed the correlation coefficient is 0.30 ± 0.01. These correlation coefficients are somewhat less than would be expected from a random bred population. They agree in showing that a fairly close relation exists between the milk production of parent and offspring in these three breeds. The results for the butterfat concentration which the cow is able to secrete in her milk are essentially similar to those for milk yield. The correlation coefficient between daughter and dam for the Holstein-Friesian is 0.41 ± 0.02, for the Guernsey 0.42 ± 0.02, and for the Jerseys 0.42 ± 0.01. The results for the butterfat percentage of the three breeds agree closely in showing that the level of the daughter's butterfat percentage is partially determined by that of her dam. They are furthermore in practical agreement with the hypothesis that the previous results have indicated, namely, the inheritance of butterfat percentage through multiple factors. It is thus shown that the inheritance of milk yield and butterfat percentage is of the same type. It remains to be shown whether or not they take place by the same factors or by different ones.

In the Holstein-Friesian breed, where there is no physiological correlation between milk yield and butterfat percentage found in the cow's milk, it is possible to approach this problem by comparing the butterfat percentages of the dam with the milk yields of the daughter; for if the same factors are responsible for determining the inheritance of both variables, then a comparison of one variable in the dam with the other in the daughter should give correlation coefficients which are of the same magnitude as those derived from a comparison of the same variable in each, whereas if the inheritance is by separate factors, little or no correlation would exist between the one record in the parent and the other record in the daughter. For the Holstein-Friesian cows there is no correlation between the milk yield of the daughter and the butterfat percentage of the dam, or the butterfat percentage of the daughter and the milk yield of the dam. These results therefore establish the conclusion that milk yield is inherited through a separate set of factors from those for the inheritance of butterfat percentage.

The amount of influence of the sire upon the production of his daughters may be determined from the fact that for any given sire the records of his daughters will all fall in one array of the correlation table. The variation of those records in relation to those of the whole population makes it possible to calculate the correlation coefficient between the production of the daughter and that of the sire, even though it is impossible to measure the sire's production. When this calculation is completed, the Holstein-Friesian sire has a correlation coefficient between the daughter and his potential record of 0.52 for milk yield; that for the Guernsey sire is 0.50. The correlation coefficients for the butterfat percentage of sire and daughter are,—for the Holstein-Friesian breed 0.53 and for the Guernsey breed

0.54. These correlation coefficients agree within practical limits with those found in the same breeds for the relation of production of daughters and dams. The sire is, therefore, equally important with the dam in determining their offspring's milk production or butterfat percentage, even though this potential inheritance is never physiologically expressed by the male.

This conclusion may be checked in another manner. Full sisters have a common sire and a common dam, half sisters have either the sire or dam in common but not both. If the sire alone or in major part determines the production of his daughter, the above relationships would lead to the expectation that full sisters would resemble each other in their production and half sisters with a common sire would resemble each other in their production to the same or nearly the same degree that full sisters are correlated. Half sisters with a common dam would not resemble each other or would resemble each other only to a slight degree. If, on the other hand, both the sire and dam determine the production of their daughters to the same or nearly the same extent, the full sisters' production would be fairly closely correlated. The half sisters' production would be correlated but to a less degree than the full sisters', and further, the correlation coefficients between the half sisters should be of the same order of magnitude. If, as a last alternative the dam determines the production, the expected relation would be,—the full sisters' production correlated; the half sisters' production, where the sire is the common parent, not correlated; half sisters with a common dam correlated in their production to the same degree as full sisters. The actual results show that full sisters resemble each other more closely in their milk yields and butterfat percentages than half sisters for the three breeds, Holstein-Friesian, Guernsey, and Jersey. The full sisters are correlated in their milk yields as follows: Holstein-Friesian, 0.55 ± 0.03; Guernsey, 0.41 ± 0.02; Jersey, 0.39 ± 0.02. Half sisters with a common sire have the following relations between their milk yields: Holstein-Friesian, 0.36 ± 0.02; Guernsey, 0.13 ± 0.02; Jersey, 0.23 ± 0.01. The milk yields of half sisters with a common dam show the following correlations: Holstein-Friesian, 0.38 ± 0.03; Guernsey, 0.15 ± 0.02; Jersey, 0.20 ± 0.01. The results for the inheritance of butterfat percentage are of similar order of magnitude,—full sisters: Holstein-Friesian, 0.46 ± 0.03; Guernsey, 0.44 ± 0.02; Jersey, 0.41 ± 0.01. Half sisters with a common sire show the following relations: Holstein-Friesian, 0.37 ± 0.02; Guernsey, 0.17 ± 0.01; Jersey, 0.25 ± 0.01. Half sisters from a common dam are correlated thus: Holstein-Friesian, 0.22 ± 0.04; Guernsey, 0.19 ± 0.01; Jersey, 0.20 ± 0.01. Full sisters resemble each other more closely in their milk yields and butterfat percentages than half sisters. The half sisters from a common sire or from a common dam have practically the same degree of resemblance. The hypothesis that the sire and dam are equally and jointly responsible for the milk productions and butterfat percentages of their offspring is consequently borne out by this comparison. The results are furthermore in accord with the expectation of a random-bred Mendelian population. For such a population the relation between full sisters should be measured by a correlation coefficient of 0.5, for half sisters by a correlation coefficient of 0.25. Actually for the three breeds averaged together the correlation coefficient for the milk yields of full sisters was 0.45 and that for half sisters 0.24. For butterfat percentage the correlation

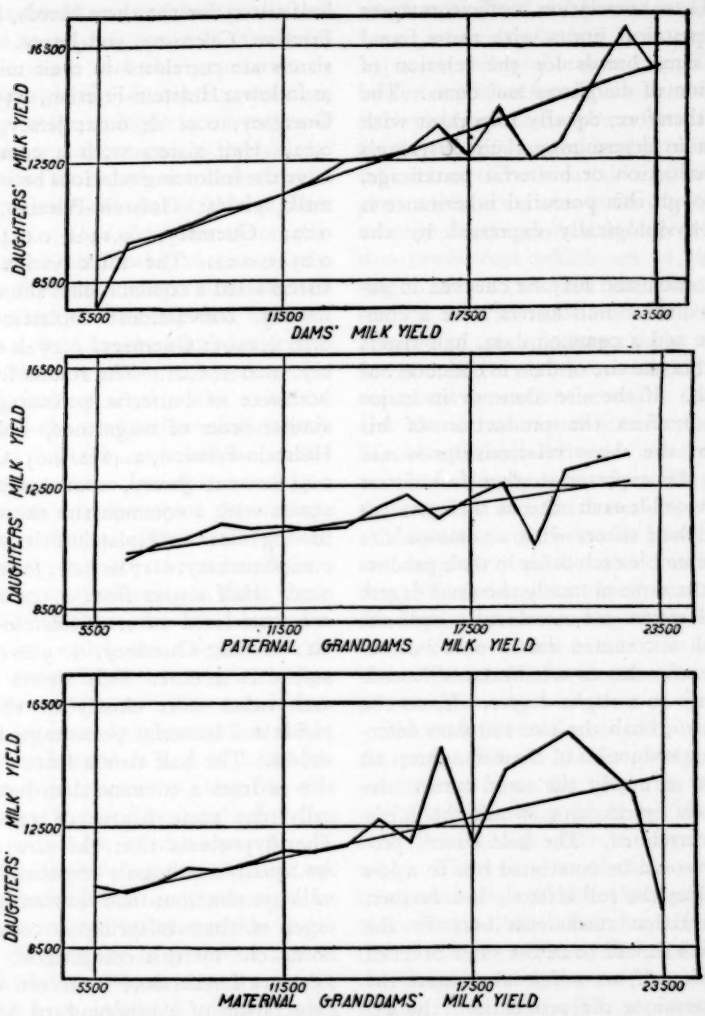

FIG. 3. AVERAGE MILK YIELDS OF DAUGHTERS OR GRANDDAUGHTERS FOR DAMS OR GRANDDAMS IN THE GUERNSEY ADVANCED REGISTRY

The upper graph shows the relation between the daughter and dam. The middle graph the relation between granddaughter and paternal granddam. The lower graph the relation between the granddaughter and maternal granddam. Examination of these graphs shows that for either type of ancestors an increase in the milk production results in an increased average production of their daughters or granddaughters. Contrasting the average production of the daughters for an increase in the production of the dams as compared with an average production of the daughters for a like increase in the production of the granddam, it is found that a given increase in the dam's production results in a much more marked average increase in the daughter's production, in fact nearly twice as great an increase in production as that found for granddam and granddaughter.

coefficient was 0.43 for full sisters and 0.23 for half sisters.

It is of interest to note that on an inheritance view, the ancestors further removed than one generation should play a prominent part in the control of the secretory activities of the mammary glands. The interrelation between the production of daughter, dam, and granddam is shown in figure 3. The upper chart shows the relation between the daughter and dam. The middle chart the relation between the granddaughter and paternal granddam. The lower chart the relation between the granddaughter and maternal granddam. Examination of these charts shows that for either type of ancestors an increase in their milk production results in an increase in the average productions of the daughters or granddaughters. Comparison of the average production of the daughters for a given increase of production in the dam with the average production of the daughter for a like increase in the production of the granddam shows that an increase in the dam's production results in a much more marked increase in the daughter's production, in fact twice as great an increase in production as that caused by the granddam. This conclusion is supported by the three breeds, Holstein-Friesian, Guernsey, and Jersey. It is true for both the yield of milk and for the butterfat percentage in the milk. The different grandparents, paternal and maternal are about equally important. In terms of correlation these relations for granddaughters' and granddams' records are,—for milk yield: paternal granddam, Holstein-Friesian, 0.26 ± 0.04; Guernsey, 0.16 ± 0.01; Jersey, 0.20 ± 0.01; for the maternal granddam, Holstein-Friesian, 0.31 ± 0.05; Guernsey, 0.20 ± 0.02; Jersey, 0.14 ± 0.02. Comparing these results with those obtained for the relation between the daughter and dam, the grandparents have about half the correlation with the daughter's production that the dam has. Similar results are obtained from the butterfat percentage. For Holstein-Friesian, Guernsey, and Jersey breeds, the paternal granddams are correlated with their granddaughters' productions to the following extent: 0.09 ± 0.04, 0.15 ± 0.01, 0.21 ± 0.01. The maternal granddams are correlated with their granddaughters' productions as follows: Holstein-Friesian, 0.19 ± 0.05; Guernsey, 0.20 ± 0.02; Jersey, 0.25 ± 0.02. The average correlation for the butterfat content of the milk of the granddams and granddaughters for the three breeds is 0.18, or the granddaughters' butterfat percentages are correlated with their granddams' butterfat percentages to about half the magnitude that they are correlated to their dams'. The mechanistic control of milk production and butterfat content, as organized within the cow, is thus in part portrayed by the performance of both the parents and grandparents.

Another ancestral combination used in dairy cattle breeding is that of cousins. The importance of this combination comes from the habit of giving a good deal of weight to the production records of the brother's daughters in selecting a bull for a herd sire. The daughters of such a bull would, of course, be cousins to the daughters of his brother. The study of this relation for both yield of milk and the butterfat percentage it contains for the Holstein-Friesian breed shows that there is a small degree of relation between the production record of one cousin and that of another. For milk yield the average relationship on the correlation scale is 0.15, for butterfat percentage the average relationship is 0.16. The quantitative

relations agree fairly well with those demanded by the Mendelian theory of inheritance through multiple factors.

A similar combination of ancestors by which further evidence for the Mendelian theory of milk production may be adduced is that of the relation between the productions of aunt and niece. This combination is used sometimes in selecting a herd bull, because of the belief that his daughters will duplicate the milk productions of his sisters. The relationship between a sire's daughters and his sons' daughters is that of aunt and niece. In making this comparison the average production of the aunt was contrasted with the average production of the nieces. The correlation coefficients measuring this relationship are,—for the milk yields of Guernsey cattle, 0.26 ± 0.02; and for butterfat percentages, 0.18 ± 0.02. These correlation coefficients agree with those expected in a Mendelian population, breeding at random and involving multiple factors.

The known facts regarding the variations of milk production may now be examined from a somewhat different viewpoint. The milk production of a cow varies from lactation to lactation. Contrasted with the other cows of the herd, the cow under consideration may in a given year be the highest producer of milk and in the following year drop in production to be the tenth highest producer in, say, a herd of fifty cows. The question may be asked what are the factors which bring about the degree of permanence of a cow's position in a given herd with respect to her milk production, for such a case as that illustrated above. A little consideration of this question shows that this permanence must be accounted for by influences which have preceded the time of milk production. The cow's heredity and environment before the lactation would be the important factors tending to stabilize the cow's production to a given level. The unstable factors would be those of environment and climatic conditions and changes of food tending to cause variation within the given lactation. In the earlier results here reported, the influence of heredity is measured. It is possible, therefore, to contrast this influence in determining the permanence of a cow's production with that found to exist in the permanence of production from one lactation to another.

For the Holstein-Friesian breed the average correlations between the records of one lactation and those of another are found to be 0.667 for milk yield and 0.715 for butterfat percentage. These correlations measure the cow's permanence in the production of milk and butterfat percentage. They measure the influence of those factors of environment which tend to cause a permanent difference in quantity or quality of milk, combined with the effect of those for heredity. The effect of the dam's contribution to the heredity of the daughter for milk yield is indicated by the correlation coefficient 0.50. The influence of the sire's contribution to the daughter's milk production is 0.52 as measured on the correlation scale. It is not possible to obtain the correlation between the sire's and dam's performance. The next best measures of this cross correlation, or the degree of assortative mating, are those between the paternal granddam's record and the record of the cow to which her son is bred, correlation 0.14, and between the two granddams' records, correlation 0.30. It will be noted that these cross correlations decrease as the animals compared approach the cow under consideration. It is therefore reasonable to suppose that the correlation of sire and dam is not more than 0.14, and probably less than this figure. From these data the total

influence of the two parents' heredity on the daughter's performance in milk yield is 0.67. The multiple correlation for the parents' and grandparents' records with the daughter's milk production is 0.68. These correlations are numerically identical in value with that measuring the degree of permanence in a cow's milk yield, 0.667. It is thus evident that it is the inheritance a cow receives which tends to make her milk production at a permanent level when contrasted with that of other cows.

The data for the butterfat percentage may be treated in the same manner. The average parental correlation for sire and dam with the daughter's butterfat percentage is 0.47; the average grandparental correlation is 0.25. The correlation for assortative mating as indicated by the relation of the butterfat percentages of paternal granddam and dam is 0.001; for the maternal grandparent's butterfat percentage it is 0.04. In other words, it is justifiable to assert that there is no true selective breeding for butterfat percentage within the breed. With these data the multiple correlation of the parents' and grandparents' butterfat percentages with the butterfat percentage of the daughter is found to be 0.67. For the parents alone the multiple correlation was 0.67. The correlation between the butterfat percentage of one lactation and that of another is 0.72. This correlation, like that for milk yield, can be interpreted as due to the influence of constant environmental conditions or heredity. The multiple correlation of the parents' and grandparents' records with that of the daughter shows that practically all of the permanence in the cow's ability to secrete butterfat percentage is due to the influence of inheritance.

SUMMARY

In this review an attempt has been made to portray the interaction of recognized biological factors leading to milk production. Milk itself is a product of great metabolic activity on the part of the mammary gland. Some of the raw materials for its synthesis are apparently dextrose, phosphatids, and amino acids, the dextrose being converted into lactose, the phosphatids into fat, and the amino acids into proteins. Individual animals vary greatly in their ability to synthesize these products and form quantities of milk or to regulate the concentration of the different constituents in the milk. When the causes of this variation are examined heredity in its broad sense is found to be the primal cause of this variation. Thus the parents or grandparents may to a large degree portray the relative milk yield or concentration of the milk solids of a given cow as contrasted with other cows. It was further shown that the relative amount of milk which was secreted and the butterfat content of the same were independent in their inheritance for Holstein-Friesian cattle. Finally the cow and her relatives were shown to be correlated in their milk productions, etc., as would be expected for Mendelian inheritance in its most generalized case, multiple factors and random mating.

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THE GROWTH OF POPULATIONS

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VARIABLES

THE primary biological variables involved in the growth of population are two in number: the force of *natality*, measured by the birth rate, on the one hand; and the force of *mortality*, measured by the death rate, on the other hand. These primary elements are fundamental to the discussion of the growth of populations of any and all organisms whatever, from *Amoeba* to man. In most of the lower organisms living in a state of nature, whether plant or animal, these are the only first-order variables which have to be taken into account in discussing the problem, and in experimental studies on population growth the arrangement of the experiments is usually such that only natality and mortality can possibly directly determine the number of individuals in the population at any given time.

In most human populations, especially those inhabiting large geographical areas, a third factor may influence directly the size of the population at any given moment, in greater or less degree. This third factor is *migration*, and it is theoretically to be regarded as a primary variable in determining the growth of such human populations.

Besides the three primary biological factors of natality, mortality, and migration which influence the observed growth of human populations there are various secondary environmental factors which may play a part in determining the final result. These are such things as food supply, the economic situation in general and in particular, social forces of various sorts, and perhaps others. But it should always be kept in mind, and this I particularly wish to emphasize, that these are all *secondary* factors from a biological point of view. They produce whatever effect they may have upon the final result, namely the size of the population at any given moment, by acting, more or less powerfully as the case may be, upon one or more of the three primary biological variables, natality, mortality, and migration. Thus an economic depression in a particular country may affect adversely the birth rate of that country, or even the death rate if the degree of the depression is sufficiently great or its duration sufficiently prolonged. These effects will, in greater or smaller degree, reflect themselves finally in the size of the population. This final effect upon the growth of the population may, however, be extremely slight, and difficult or even impossible of separate statistical recognition or measurement, because of compensating influences at work at the same time. Logically, however, the operation of these secondary factors must always be recognized. But from the point of view of the theory of population growth their influence is always a second order one. They can produce any effects upon population only by operating upon the primary biological forces of natality, mortality, and migration.

HOW POPULATIONS GROW

It is an observed *fact*, which at this stage of the discussion involves no theoretical implications whatever, or postulates special to it, that the growth of populations of the most diverse organisms follows a regular and characteristic course. In general and everyday terms of common sense this characteristic manner of population growth may be described in the following way. The population at first grows slowly, but gains impetus as it grows, passing gradually into a stage of rapid growth, which finally reaches a maximum of rapidity. After this stage of most rapid growth the population increases ever more and more slowly, until finally there is no more perceptible growth at all. In short, the populations of various forms of life first wax in their speed of growing and then wane.

This characteristic phenomenon may be more precisely described in a variety of ways, depending upon which of several mathematical aspects of the matter we choose to stress. This may best be illustrated by a concrete example. For this we may well take a relatively simple case biologically, such as is afforded by the growth of a population of yeast cells. The yeast plant is an organism low in the scale of life. Its reproduction, under the conditions of the experiments, is by the process of cell division, the cells present at any given moment forming new cells by budding. An experiment on the growth of a population of yeast cells is made as follows: A measured amount of wort, which furnishes nutriment to the yeast plants, is seeded with a few cells. Then at equal intervals of time thereafter the equivalent of a census count is made of the cells then present. Because of the minute size of the individual cells, and of other technical difficulties, some sort of indirect method is commonly used to measure the size of the population, in place of direct counts. But this is a matter merely of detail, which need not detain us in the present discussion.

The outcome of a typical experiment of this sort, the data being taken from an investigation of the subject made by Carlson (3), is shown in table 1. A further discussion of these data will be found in an earlier work (8). The figures of columns (*b*) and (*c*) are shown graphically in figure 1.

TABLE 1

Growth of a population of yeast cells (data from Carlson)

HOURS OF GROWTH	QUANTITY OF YEAST		ABSOLUTE QUANTITY OF YEAST PRODUCED PER HOUR (= TIME RATE OF GROWTH)	QUANTITY OF YEAST PRODUCED PER HOUR IN PER-CENT OF TOTAL UP TO THAT HOUR (= PER-CENTAGE RATE OF GROWTH)
	OBSERVED	CALCULATED		
(*a*)	(*b*)	(*c*)	(*d*)	(*e*)
				per cent
0	9.6	9.9		
			8.7	90.6
1	18.3	16.8		
			10.7	58.5
2	29.0	28.2		
			18.2	62.8
3	47.2	46.7		
			23.9	50.6
4	71.1	76.0		
			48.0	67.5
5	119.1	120.1		
			55.5	46.6
6	174.6	181.9		
			82.7	47.4
7	257.3	260.3		
			93.4	36.3
8	350.7	348.2		
			90.3	25.7
9	441.0	433.9		
			72.3	16.4
10	513.3	506.9		
			46.4	9.0
11	559.7	562.3		
			35.1	6.3
12	594.8	600.8		
			34.6	5.8
13	629.4	625.8		
			11.4	1.8
14	640.8	641.5		
			10.3	1.6
15	651.1	651.0		
			4.8	0.7
16	655.9	656.7		
			3.7	0.6
17	659.6	660.1		
			2.2	0.3
18	661.8	662.1		

In table 1 the first column (*a*) gives the hours during which growth occurred; the second column (*b*) records the observed quantity of yeast, or in other words the size of the population, at each successive

hour; the third column (*c*), which may be neglected for the present, gives the size of the population at each successive hour as calculated from a mathematical equation to be discussed later; column (*d*) gives the simple time rate of growth, that is the absolute amount of new yeast produced by the growth of the population in each successive hour. The figures in this column are the observed values of the

Column (*d*) tells us that in the growth of this yeast population the absolute increment of new yeast cells per unit of time *increases* each hour as the population grows, up to a maximum increment per hour, which is attained in this case somewhere about the 7th or 8th hour. Thereafter as growth continues the absolute increment of new cells per unit of time *decreases* hour by hour until it almost

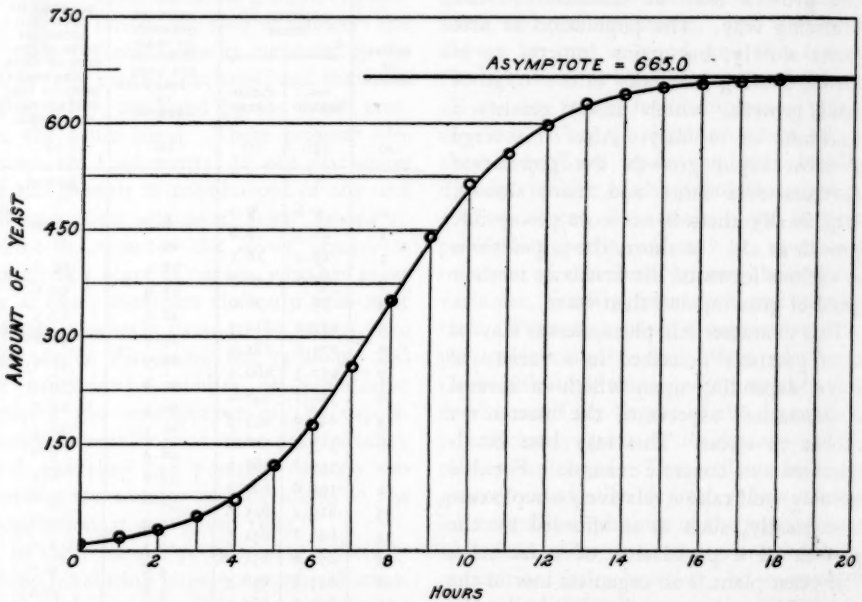

FIG. 1. THE GROWTH OF A POPULATION OF YEAST CELLS

In the publication of this diagram in (8), through an error in proof-reading the abscissal units were stated to be days, when they should have been hours, as is correctly shown here. (Data from Carlson.)

ratio dy/dt, y denoting the size of population and t denoting time in hours. The last column (*e*) gives the relative rate of growth, in proportion to the already attained size of the population, in each time interval. In mathematical terminology the figures in this column are the observed values of the double ratio $\frac{1}{y} \cdot \frac{dy}{dt}$ for each hour.

vanishes, and, for all practical purposes, the population has ceased to grow.

If the figures of column (*d*) are plotted, as in figure 2., they obviously form a curve shaped like a cocked hat or sugar-loaf, low at the two ends and rising to a peak near the middle. As a natural consequence of this trend of the first differences the relative growth rates given in column (*e*) are found to be largest at the

start of growth and to become smaller as the absolute size of the population increases. Although this relative rate of growth presented in column (*e*) is the one most often discussed by demographers in talking about population growth, it tells us much less clearly what is the real nature of the characteristic curve of such growth than does the simple time rate, or first derivative of the population growth curve given in column (*d*).

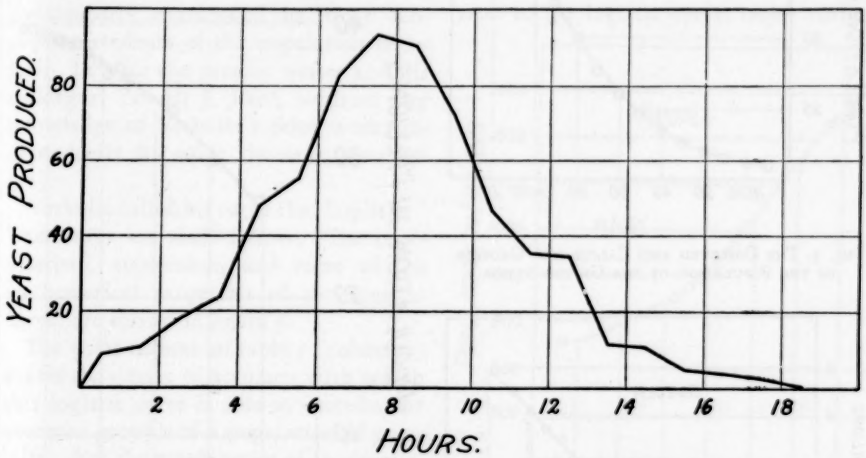

FIG. 2. GROWTH INCREMENTS OF YEAST POPULATION IN SUCCESSIVE TIME INTERVALS
Data from column (*d*) of table 1

The phenomenon shown in column (*d*), namely that the absolute increment of growth per unit of time increases with time to a maximum value, and then decreases till the end of measurable growth is reached, has been found in recent years to be the way in which populations of such a wide variety of organisms actually grow, that it may now be fairly regarded as the characteristic, normal mode of population growth, to at least a first approximation. I shall not take the time here to review all the evidence that this is so. This has already been done in two recent books (6, 8). It has been shown that experimental populations of yeast, of bacteria, and of the fly *Drosophila melanogaster*, in their growth follow this characteristic curve with great precision.

Furthermore it has been demonstrated statistically that populations of human beings have grown according to the same type of curve, so far as may be judged from the available census records, in at least the following countries: Sweden, United States of America, France, Austria, Belgium, Denmark, England and Wales, Hungary, Italy, Norway, Scotland, Servia, Japan, Java, Philippine Islands, Baltimore City, New York City, and the world as a whole.

In illustration of this statement four cases are presented graphically here. These are the United States (fig. 3), Sweden (fig. 4), France (fig. 5), and the world as a whole (fig. 6). In these diagrams the circles give the census counts (or, in the case of the world as a whole, estimates) of the populations existing at

the given dates, while the smooth curves are the fitted theoretical curves of population growth.

In the case of the demographic units listed above the census records do not extend over a sufficiently long time to make the case conclusive that population growth, if undisturbed, would follow in human groups the complete course exhibited by the yeast population just discussed. The available data only make such a conclusion in some degree probable. And one cannot conduct experiments with human beings on this point, as can be done with lower organisms. But fortunately it has been possible to find one group of human beings, the indigenous native population of Algeria, in which a cycle of population growth has been practically completed during the period for which census records are available, these having been carefully made by the French. In this case the human population followed in its whole cycle of growth a curve of the same characteristic form that has been discussed for the yeast. This case has been fully described and

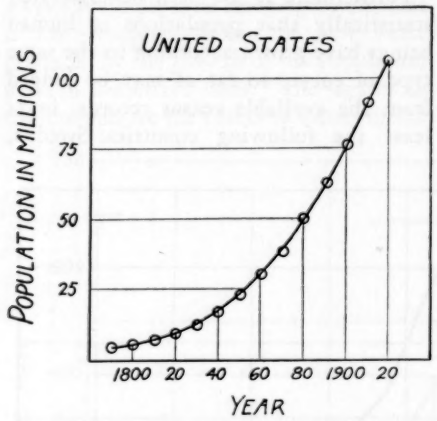

FIG. 3. THE OBSERVED AND CALCULATED GROWTH OF THE POPULATION OF THE UNITED STATES

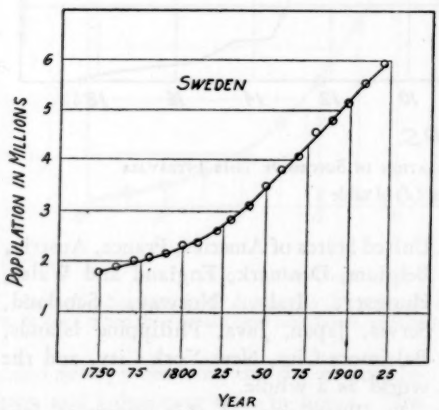

FIG. 4. THE OBSERVED AND CALCULATED GROWTH OF THE POPULATION OF SWEDEN

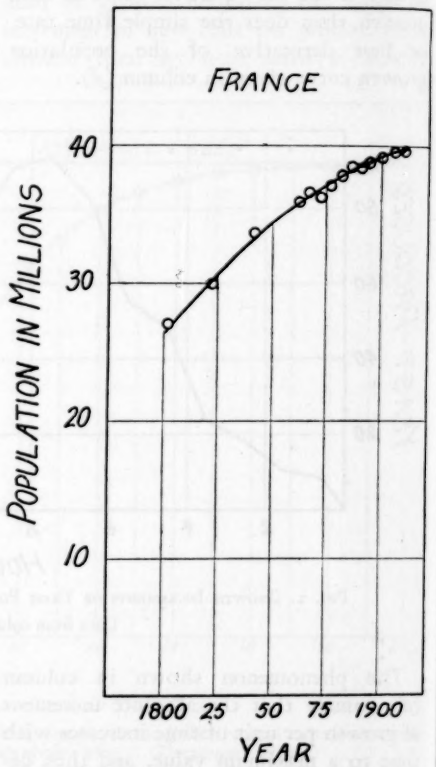

FIG. 5. THE OBSERVED AND CALCULATED GROWTH OF THE POPULATION OF FRANCE

analyzed in my book *The Biology of Population Growth* (8), and is illustrated here in figure 7.

THE LOGISTIC CURVE

The equation to the curve which has been found by experiment and observation to be descriptive of population growth in a wide variety of organisms was first discovered by the Belgian mathematician, Verhulst (18, see also 19, 20) in 1838. His pioneer work was forgotten, and consequently overlooked by most subsequent students of the population problem. In 1920 the present writer and his colleague, Lowell J. Reed, without any knowledge of Verhulst's prior work, independently hit upon the same equation (12).

Verhulst called his curve the "logistic." This usage we shall follow. The characteristic appearance, and some of the mathematical properties of the logistic curve, are shown in figure 8.

The third column of table 1 (column *c*) shows the degree of accuracy with which this logistic curve is able to describe the observed growth of a population of yeast cells. For the whole series of 19 observations the root mean square deviation between the experimental results and the theoretical curve is only 3.59. The equation of the fitted curve is:

$$y = \frac{66.5}{1 + e^{4.1896 - 0.5335x}}$$

where y = quantity of yeast, and x = time of growth in hours.

The possession of such a curve as this, which is found by actual experience to describe accurately the course of population growth in a wide variety of organisms, is a valuable first step, but only a first step, towards reaching an understanding of the biology of the process. What we want to know is how the biological forces of natality and mortality are so integrated and correlated in their action as to lead to a final result in size of population which follows this particular curve rather than some other one. This demands that we shall push the enquiry further.

MATHEMATICAL CONSIDERATIONS

There are two lines along which this further investigation must proceed. The first is a theoretical mathematical analysis of the relation of birth rates and death rates to the logistic curve, under various

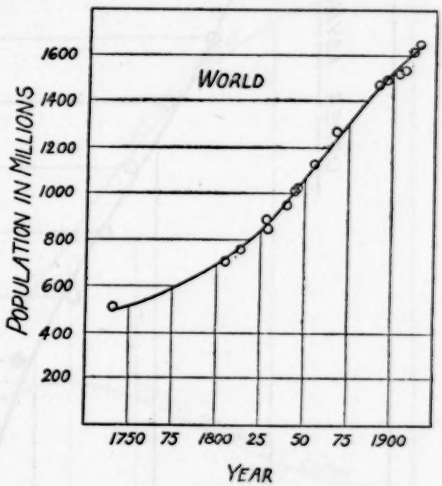

FIG. 6. THE OBSERVED AND CALCULATED GROWTH OF THE POPULATION OF THE WORLD

postulates. We have done a considerable amount of work, as yet unpublished, upon this subject. Certain aspects of it have also been discussed by Yule (25) and Lotka (5). I shall not attempt to present the details of this analysis on this occasion, because of their technical character. Some of the results, however, may be stated in simple form and are pertinent to the present discussion.

It is easily shown that if birth rates and death rates are assumed to remain constant, at any values consistent with growth at all (i.e., birth rates larger than

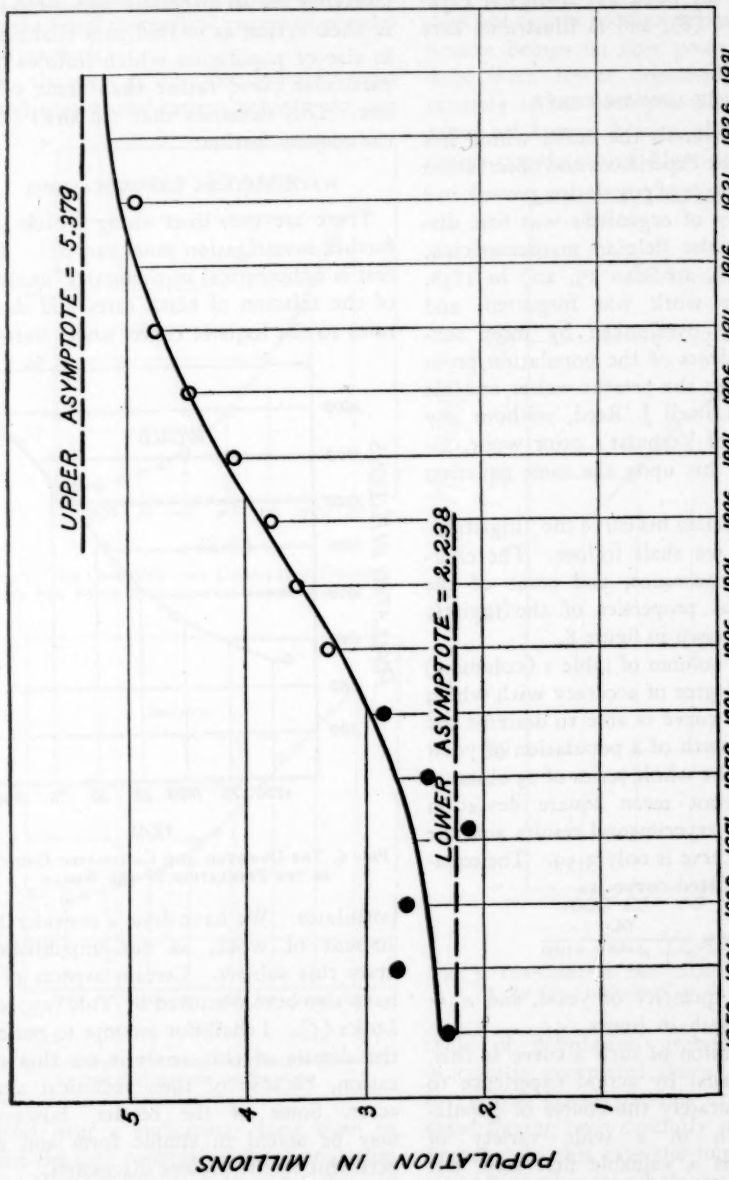

FIG. 7. OBSERVED AND CALCULATED GROWTH OF THE INDIGENOUS NATIVE POPULATION OF ALGERIA

death rates) the population will grow according to an exponential curve, on to infinity. The rate of this progression may be slow or rapid according to the assumptions made, but the form is exponential. Nothing like the slowing down of growth after a period, which is seen in the logistic curve, appears under this postulate.

But plainly, with actual populations of living organisms, birth rates cannot continue constant indefinitely. In saying that birth rates shall be constant regardless of the size of the population already attained, it is tacitly, but implicitly, assumed that the universe in which the hypothetical population is growing expands proportionately with this growth, so that each single element always has plenty of room, no matter how large the whole group becomes. But such an assumption is unwarranted for any actual population whatever. All populations of real organisms live in universes with definite limits. The absolute size of the universe may be small, as in the case of the test-tube which holds the yeast cells, or it may be as large as the earth, most of which could conceivably be inhabited, on a pinch, by man. But in any and every case there is ultimately a definite limit to the size of the universe in which any real population lives.

This consideration obviously alters the

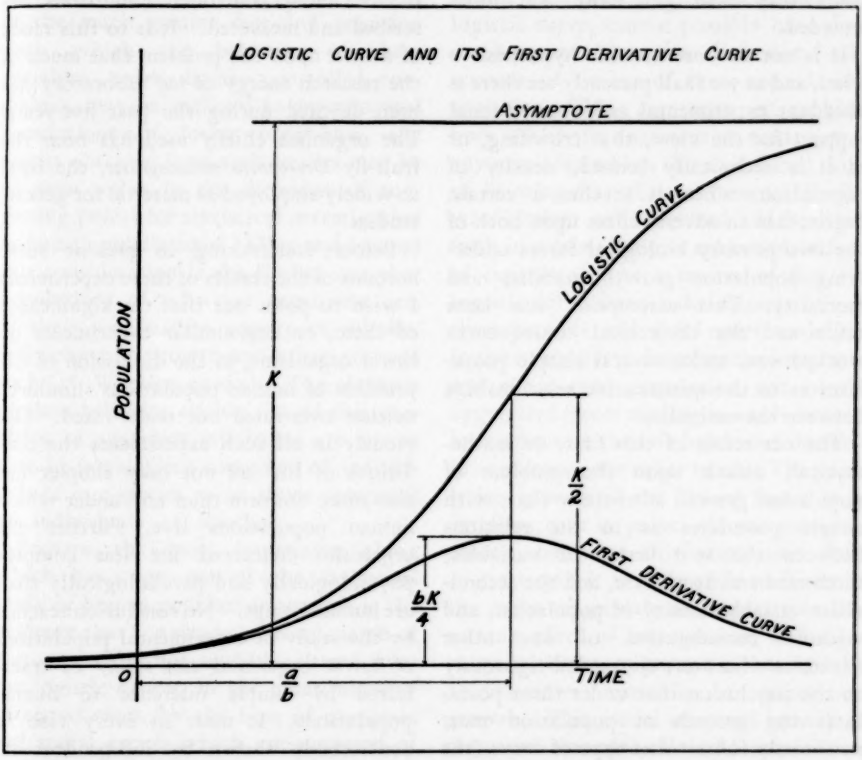

FIG. 8. THE LOGISTIC CURVE AND ITS FIRST DERIVATIVE

complexion of the case. For it at once follows that if the universes in which populations live are finite and inextensible, there must come a time in the growth of any population when the individuals composing it begin to get crowded, and as the growth continues beyond this point they will get more and more crowded.

It is not an unreasonable hypothesis *a priori*, and as we shall presently see there is abundant experimental and observational support for the view, that crowding, or as it is technically termed, density of population, when it reaches a certain degree, has an adverse effect upon both of the two primary biological forces underlying population growth, natality and mortality. This assumption has been made and the theoretical consequences worked out, under several simple postulates as to the quantitative relationships between the variables.

The net result of this first, or mathematical, attack upon the problem of population growth is to show that, with simple postulates as to the relations between the two first-order variables, birth rate and death rate, and the second-order variable density of population, and without consideration of any other variables whatever, we are led rigorously to the conclusion that under these postulates the growth of population must necessarily follow that type of curve (the logistic) which is empirically found to describe the growth of actual populations of widely diverse organisms.

EXPERIMENTAL POPULATIONS

The second mode of attack upon the problem of the biology of population growth is the experimental. Its purpose is to observe at each stage the growth of the population of some actual organisms, small enough to be capable of laboratory management, under carefully controlled and known conditions. Not only can the growth of such an experimental population as a whole be observed, but also it is possible to set up experiments in which each separate variable such as natality, mortality, density of population, etc., can be particularly studied, and its behavior under controlled conditions described and measured. It is to this mode of attack upon the problem that much of the research energy of my laboratory has been devoted during the past five years. The organism chiefly used has been the fruit-fly *Drosophila melanogaster*, the form so widely employed as material for genetic studies.

Before undertaking to present some account of the results of these experiments I wish to point out that the significance of these, or any similar experiments on lower organisms, in the discussion of the problem of human populations should be neither over-rated nor under-rated. Obviously in all such experiments the conditions of life are not only simpler but also more uniform than any under which human populations live. Further the organisms concerned are less complex physiologically and psychologically than are human beings. No conclusion reached by the study of experimental populations of lower organisms can safely be transferred by simple inference to human populations. It must in every case be conclusively shown by independent investigation of human populations that the same conclusion holds for them, if it does. Furthermore if the same result is, in fact, found to appear in both experimental and human populations, by no means may it safely be inferred that the causes leading to this result are necessarily the same in the two cases. They may be or they may not. To find out which alternative is true demands special *ad hoc* investigation.

On the other hand it must also be kept

in mind that the forces of natality and mortality are basic biological attributes of aggregates of living things, men as well as flies. The ultimate biological forces leading to the observed growth of a human population are these two, natality and mortality, just as truly as they are in a population of flies or yeast cells. Because of the much greater ease and precision with which the behavior of these variables, under diverse controlled conditions, may be analyzed in experimental populations of lower organisms, the results obtained from such studies may be of great value in the direction of suggesting points for statistical investigation in human populations. Over and beyond this consideration is the further one that populations of whatever organisms are, in their very nature, aggregate wholes, and behave in growth and other ways as such (cf. Wheeler, 21–24). The elements of their behavior arising out of this condition of aggregate wholeness are just as true in populations composed of individuals of one species as in those composed of individuals of another.

Perhaps the most impressive thing which has come out of the statistical study of human populati on growth is the evidence that the steady onward march of this growth is not sensibly altered from the logistic course, in the great majority of actual cases, by the host of economic and social events which are supposed of logical necessity to affect it. This statement should not be taken to mean that economic and social factors are unimportant in their relation to population growth. So far am I from holding any such opinion that it is my belief that economic forces are probably the most important single element in the biologically effective environment of civilized man today. All that is meant is that, in the majority of observed cases at least, the effect of these factors on human population growth *has in the past, at any rate, been such as to make the growth of the population follow the logistic curve, rather than deviate from it.* During the past few years the argument has been made that the very populations which have in fact grown with great precision according to a logistic curve, cannot possibly have done so, because this curve does not "take account of" a lot of these second-order variables. This argument is rubbish, born out of the conservative resistance to any new idea which the established order of learning has always shown, by that wind-broken and spavined old stallion, faith in *a priori* logic as against plain facts of experience. As a matter of fact the logistic curve does "take account of" all these second- and third-order variables, in the sense that it describes the integrated end effect upon population size of the aggregated forces tending towards increase in numbers on the one hand, and decrease in numbers on the other hand. The population growth of the United States is an excellent case in point. If one plots the census counts of this population from 1790 to 1920 it is impossible to detect in the curve of growth any separate or disturbing effect of immigration, although, as we have seen, migration is theoretically a first-order variable in population growth. The actual observed growth of the population of the United States follows the logistic curve with remarkable precision. To suit various theorists it presumably ought not to, but *in fact* it does. Benjamin Franklin long ago pointed out that for the growth of population aggregates of any considerable size migration was an unimportant factor, as compared with natural increase by reproduction. He was right. Whatever the future may develop, the past history of the matter shows plainly that human populations

have behaved in their growth in the same way that experimental populations of lower organisms do, with truly remarkable faithfulness.

DROSOPHILA POPULATIONS

The details of the technique of making experiments on population with the fly *Drosophila melanogaster* have already been described (8), and need not be repeated here. It will suffice to say that in bottles of measured size definite amounts of food material are placed, and then an initial group of a few flies—say one male and one female—is added. At regular intervals thereafter the then existing population in each bottle is carefully counted and recorded, and the individuals composing it returned to the bottle to carry on their normal lives until the next census count.

TABLE 2

The growth and decline of a hypothetical population assumed to start with two individuals and to be subject thereafter to the indicated birth and death rates

PERIOD	PERCENTAGE BIRTH RATE IN PERIOD	BIRTHS IN PERIOD	PERCENTAGE DEATH RATE IN PERIOD	DEATHS IN PERIOD	POPULATION AT BEGINNING OF PERIOD
1	100	2.0	10	0.2	2.0
2	90	3.4	20	0.8	3.8
3	80	5.2	30	1.9	6.5
4	70	6.8	40	3.9	9.7
5	60	7.6	50	6.3	12.6
6	50	6.9	60	8.3	13.9
7	40	5.0	70	8.7	12.5
8	30	2.6	80	7.0	8.7
9	20	0.9	90	3.9	4.4
10	10	0.1	100	1.3	1.3

There are several ways in which an experiment on the growth of a *Drosophila* population can be carried out. Some of these ways differ in principle in a manner that is of importance in determining the kind of result obtained. The simplest case is to set up an experiment in the way described briefly above, and thereafter literally do nothing further except to let nature take its course and to count the flies at intervals. What then happens is that the population grows along a logistic curve for a little more than half of a complete cycle of such a curve. Then quite suddenly the population begins to decrease in numbers. This decrease goes on at an accelerating rate, until there are no survivors left.

The result is precisely that which is to be expected mathematically on the postulates that birth rates decrease and death rates increase uniformly at a constant linear rate. This is shown in table 2.

In the actual experiments the changes in the birth and death rates which lead to this type of curve, with first growth and then decline of population, are directly associated with the diminishing food supply under the conditions of a limited and closed universe.

The second type of experiment is one in which an attempt is made to add food as the supply is used up. The technical difficulties of doing this satisfactorily with a *Drosophila* population are considerable, but by sufficient care they can be overcome in large degree. The resulting growth of the population then follows a simple logistic curve, as I have described in detail elsewhere (8), and as is shown graphically in figure 9. There are two points in connection with experiments of this type which seem to need emphasis in the light of further work. The first is that, owing to the technical difficulties of adding new food to a bottle for reasons that are fully discussed in the reference cited, the food conditions are always suboptimal in experiments of this type. The second point is that the smoothness with which the populations follow the logistic curve in this type of experiment is probably a direct consequence of the fact just mentioned that the conditions as to food

are definitely sub-optimal. The nutritional level of the bottle is not high. It only a little more than barely permits *continued* growth of the population. Under these circumstances violent oscillations of either birth rates or death rates do not occur. The observations of population size lie smoothly on the logistic curve until the asymptote is nearly reached.

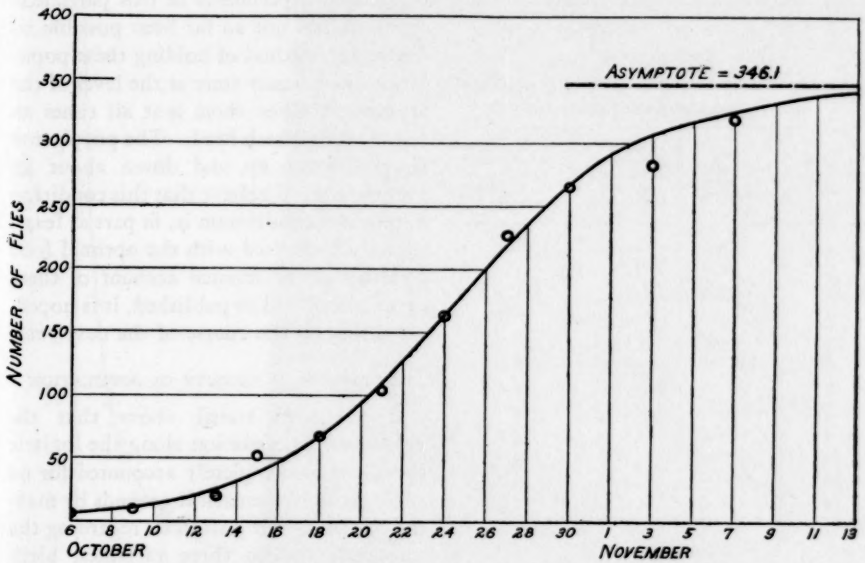

FIG. 9. GROWTH OF AN EXPERIMENTAL POPULATION OF DROSOPHILA

The circles are observed census counts, and the smooth curve is the fitted logistic. (From Pearl (8))

The third type of experiment, which I here report on in a preliminary way for the first time, is so planned as to have the food conditions always optimal both as to quality and quantity. This is accomplished in the following way. Suppose a bottle A_1 to be prepared with our new synthetic food (9), which has been shown experimentally to lead to lower death rates and higher birth rates than any other natural or laboratory food tried, and to be seeded with an initial small population. At the end of three days a census count is taken and the population is transferred to a new bottle, A_2, containing fresh new food to the same amount as was present initially in A_1. At the end of another three days a census count is again taken and the population again transferred to another bottle, A_3, which again contains new fresh food, and so on indefinitely. Meantime the lag bottles, A_1, A_2, etc., which the adult population has left by transference, are examined daily. Whenever in any such bottle any flies hatch out from eggs which were laid by the females of the adult population while they were resident in that bottle, these newly hatched flies are counted (as births) and added to the adult population in whatever bottle it happens then to be. So then we get a record of the daily birth rate of the population. Also each day the bottle is examined in which

the adult population is actually then resident, and the deaths recorded. So then the situation in these experiments is that (*a*) there is a new and abundant crop of fresh food every three days, (*b*) all the young are born in a lying-in hospital and transferred to and counted into the general population only after they have been born and dried off there, and (*c*) there is complete registration of both births and deaths, as well as census counts of the population as a whole. The population is dependent upon any given single food supply only over a period of three days. During so short a period even the largest populations obtained do not begin to exhaust the food.

TABLE 3

Experimental data on the influence of density of population on rate of reproduction in Drosophila

PAIRS PER BOTTLE AT START	MEAN POPULATION 16 DAYS AVERAGE	IMAGOES PRODUCED PER FEMALE PER DAY. OBSERVED	CALCULATED NUMBER OF PROGENCY PER FEMALE PER DAY
1	2.00	21.4	21.1
2	3.40	12.6	14.5
3	5.50	10.8	10.2
4	7.32	9.1	8.1
5	9.29	5.9	6.7
6	10.29	6.8	6.2
7	11.51	5.2	5.6
8	14.48	4.6	4.6
9	16.62	4.1	4.0
10	18.74	3.1	3.6
12	21.70	3.5	3.1
15	26.02	2.3	2.5
20	34.02	2.2	1.8
25	47.75	1.0	1.1
30	47.73	1.2	1.1
50	90.66	0.33	0.34

Many experiments of this type have been performed. The general result is that the population first grows up to a maximum or asymptotic level, just as in the second type of experiment described above. But in this case the population can be kept at this asymptotic level as long as the experimenter desires. A striking result, however, is that both during the growth period and thereafter there are violent oscillations of the populations in size, about its mean position as given by the fitted curve. In fact these waves in the size of the population, produced by oscillations in the birth and death rates, are perhaps the most characteristic feature of population experiments of this particular type. It has not so far been possible to devise any method of holding these populations in a steady state at the level of the asymptote, when there is at all times an abundance of fresh food. The population simply waves up and down about an average size. I believe that this condition of unstable equilibrium is, in part at least, causally connected with the optimal food conditions. A detailed account of these experiments will be published, it is hoped, some time in the course of the next year.

THE EFFECTS OF DENSITY OF POPULATION

It has been stated above that the growth of a population along the logistic curve can be completely accounted for on theoretical mathematical grounds by making certain simple postulates regarding the relations between three variables, birth rate, death rate, and density of population. The basic postulate was that increasing density of population has associated with it adverse changes in birth rates and death rates. Is there experimental evidence in support of such a postulate?

For several years an intensive experimental investigation has been going on in my laboratory regarding the effect of density of population upon natality and mortality in *Drosophila*. The chief results of these studies may be briefly reviewed.

Some years ago Pearl and Parker (11) showed that if a count were made of the progeny (adult flies or imagoes) produced

in bottles of uniform size, uniform amount of food, and uniform air space, but with varying densities of population, the results were those shown in table 3.

These results are shown graphically in figure 10.

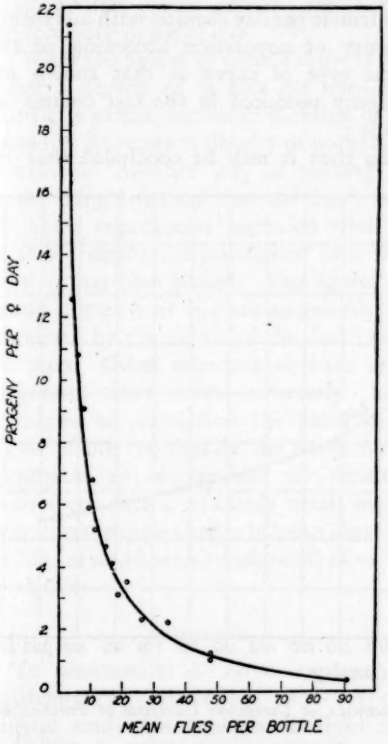

FIG. 10. SHOWING CHANGES IN RATE OF REPRODUCTION OF DROSOPHILA WITH INCREASING DENSITY OF THE MATED POPULATION

The circles give the observations and the smooth curve is the graph of the logarithmic equation discussed in the text.

There is evidently a profound and regular change in the rate of reproduction of *Drosophila*, under the conditions of these experiments, with increasing density of population. The number of progeny produced per female per day declines as density increases, at first extremely rapidly and then more and more slowly at higher densities. The total number of progeny flies (23,922) is large enough to give confidence in the results.

The last column of table 3 gives the calculated ordinates of the equation, fitted to the observations by the method of least squares,

$$\log y = 1.54 - 0.008\,x - 0.658 \log x$$

TABLE 4

Mean duration of life of Drosophila at different densities of population

INITIAL DENSITY	WEIGHTED AVERAGE MEAN DENSITY TO WHICH FLIES HAD BEEN SUBJECTED UP TO TIME OF DEATH	MEAN DURATION OF LIFE IN DAYS
2	1.77	27.31 ±0.58
4	3.30	29.32 ±0.60
6	5.00	34.45 ±0.65
8	6.68	34.20 ±0.61
10	8.15	36.22 ±0.72
12	9.72	34.31 ±0.61
15	12.42	37.92 ±0.66
20	16.69	37.07 ±0.55
25	20.68	37.47 ±0.49
35	28.85	39.43 ±0.67
45	37.23	37.46 ±0.51
55	44.65	40.04 ±0.53
65	53.16	35.25 ±0.45
75	59.66	32.34 ±0.46
85	66.95	30.10 ±0.36
95	74.50	27.17 ±0.36
105	80.36	24.20 ±0.32
125	94.38	19.60 ±0.28
150	111.88	16.17 ±0.24
200	144.47	11.93 ±0.20

where y denotes number of progeny flies produced per female per day over a sixteen-day period, and x denotes mean density of the mated population (measured as flies per bottle).

It is at once apparent that this equation describes the observed facts with extraordinary precision. Rarely, even in a physical or chemical experiment, does one get closer agreement between ob-

servation and theory than is here shown. Plainly the curve is the expression of the law relating these two variables, rate of reproduction and density. It is the inverse of Farr's law relating death rates and density in human populations (4, 1, 2).

These experimental results on the effect of density of population on the birth rate have been confirmed many times in my laboratory (*cf.* 10).

In all of these experiments so far mentioned the effect of density upon birth rates was measured by counts of adult progeny flies (imagoes) produced. This procedure left in doubt the point as to whether density produces its effect through an alteration of fecundity (egg production) or at some later stage in the process of reproduction. This doubt has now been cleared up by an elaborate series of experiments carried out in my laboratory during the past year by Dr. Arata Terao. In these experiments careful counts were made of the number of eggs produced under different densities of population. The results will shortly be published in detail. Here it is only necessary to say that they show conclusively that the primary effect of density, in populations of *Drosophila*, is upon fecundity (number of eggs laid). The number of eggs produced per female per day *decreases* with advancing density of population according to the same type of curve as that shown for progeny produced in the last column of table 3.

So then it may be concluded that increasing density of population does in fact have associated with it in experimental populations of *Drosophila* just the sort of adverse changes in the birth rate which were postulated in the theoretical discussion in the preceding section of this paper. Elsewhere (8) evidence has been presented showing that the same kind of effect of density is observable in populations of other organisms.

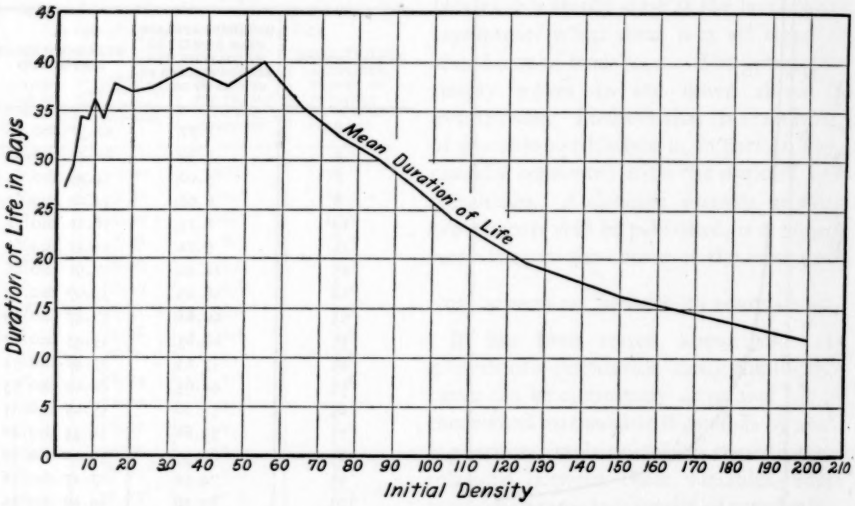

FIG. 11. MEAN DURATION OF LIFE OF WILD TYPE DROSOPHILA AT DIFFERENT DENSITIES OF POPULATION

The results of a large amount of experimental work regarding the effect of den-

sity of population upon *mortality* have recently been published in detail. Only the broad outcome can be presented here. This is done in table 4, which gives the mean duration of life in days of *Drosophila* subjected to the indicated densities of population. The experiments involved 13,000 flies. The results are shown graphically in figure 11.

What the figures in table 4 show is that after a density of 55 flies per one-ounce bottle is passed, the mean duration of life steadily decreases as density of population increases. Another way of putting the same thing is to say that the death rates in these experiments increased with increasing density of population after density 55 has been passed. The figures for mean duration of life are necessarily determined by the values of the death rates at ages. Other experiments have demonstrated that with extremely high densities of population the mean durations of life (or equally the death rates) approach an asymptote. In densities below 55, after a relatively small initial rise, there is little change in mean duration of life (or death rates) with small increases in density.

SUMMARY

To summarize: A large amount of mathematical, statistical, and experimental study has brought to light the following broad facts regarding the general biology of population growth:

1. Populations of organisms of the most diverse kinds, ranging from bacteria and yeast to man, are found statistically to follow in their growth a particular type of curve, the logistic.

2. Mathematical investigation shows that a curve of this type is necessarily generated under certain simple postulates as to the inter-relations between the two first-order variables, birth rates and death rates, and the second-order variable, density of population. One particular set of such postulates is that it shall be assumed, first, that birth rates are markedly affected adversely by small increases in density at relatively low densities, while after a certain density is passed further increases produce only slight decreases in birth rates down to an asymptotic limit; and, second, that death rates are insignificantly affected by increasing density at relatively low densities, while after a certain density is passed death rates markedly increase with increasing density up to an asymptotic limit.

3. Experimental investigation of populations of *Drosophila melanogaster* under controlled conditions shows that in fact the relations between density of population and birth rates, on the one hand, and density and death rates, on the other hand, which actually exist in such populations, are in accord with those theoretically assumed in the preceding paragraph. In short it is possible to account for all the main features of the growth of experimental populations of *Drosophila* by a simple hypothesis as to the correlated behavior of three variables.

A great deal more work needs to be done on the problem, and the investigations are being continued in my laboratory. The present paper is to be regarded only as a progress report. In condensed form it was read at the World Population Conference in Geneva, August 31, 1927, under the title "The Biology of Population Growth." It has been revised for publication in the QUARTERLY REVIEW OF BIOLOGY, and this publication is to be regarded as the definitive form of the paper.

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HOW NEAR IS THE RELATIONSHIP OF MAN TO THE CHIMPANZEE-GORILLA STOCK?

ADDRESS DELIVERED BEFORE THE SOCIETY OF MAMMALOGISTS, APRIL 29, 1927

BY WILLIAM K. GREGORY
American Museum of Natural History

IT IS almost an axiom nowadays that to be orthodox in science one must make measurements and express his results in numbers. The old-fashioned sciences of comparative anatomy, classification and phylogenetics, partly because they did not make use of statistical methods of research, have been more or less despised and neglected by the younger generation and excluded from the elect company of the "exact sciences." But I would point out that arithmetic is not the sole branch of mathematics. Even historical sciences such as geology and palaeontology may claim an humble place in the mathematical hierarchy in so far as they succeed in discovering the sequence and relationships of events in time or space. When one determines that *a* is nearer to *b*, either in space, in time, or in a degree of similarity, than it is to *c*, and that *a*, *b*, *c*, are all nearer to each other than any of them is to *m*, *n*, *o*, then, provided always that his determinations are approximately correct, he has at least opened the way for a more precise evaluation of terms in the future.

The science of phylogenetics has sometimes been treated as an idle speculation, because it is supposed to be unable to test its hypotheses by direct experimentation. But a somewhat similar disadvantage lies upon the Egyptologist, who has nevertheless succeeded tolerably well in deciphering the documents available to him. An advantage of direct experimentation is that by means of the control experiments one can compare opposite conditions. But in historical sciences such as geology and phylogenetics the opposite to a given condition must be sought in nature. Nevertheless in many instances nature does provide the control experiment. In the study of mammalian evolution for example, we find that even today there are not a few animals in every large group that retain much of the primitive pattern that is known in their remote fossil relatives. These "living fossils," such as the existing opossum, correspond at least in part to the unmodified "control experiments" of the laboratory, while their highly specialized relatives, such as the kangaroos and the wombats, are nature's successful experiments in adapting an originally arboreal type to widely different methods of locomotion. Among the order of Primates, including all the known fossil and living types, there is an imperfect but still decipherable record of the branching out of a very remote stock of Upper Cretaceous and Paleocene age, from forms in general like the modern tree-shrews, into the various divisions of lemurs, cheiromyoids, lorisoids, tarsioids, platyrrhine monkeys, Old World monkeys, anthropoids and man.

At the present time the chimpanzee and

the gorilla differ from man in so many striking characters that Professor Osborn has recently written that the human family has been totally disconnected from the Simiidae since its earliest infancy. Denying the "myth" of man's descent from apes as due to our ignorance of the real course of human evolution, Professor Osborn holds that the existing apes have ape brains and ape minds, adapted for life in

FIG. 1. GORILLA FOETUS
(After Deniker)

the forest, that they walk on all fours, that the human foot shows no evidence of derivation from an arboreal type, that when men climb they do so in an awkward un-ape-like fashion, that the Neanderthal race had descended from thousands of generations of upright-walking men, and finally, that man was already a tool-making, intelligent being in the Pliocene epoch, certainly more than one million years ago.

LIKENESSES OF MAN AND ANTHROPOIDS

In the face of this crushing indictment can anyone continue to defend the claim of the gorilla and the chimpanzee to be man's next of kin? Profoundly as I regret to differ from Professor Osborn, I must testify that my own studies of recent and fossil vertebrates have led me to somewhat different conclusions regarding the origin of man. In brief, as it appears to me, there is cumulative evidence for Darwin's view that man represents an early offshoot from the anthropoid stock, that he is descended from a thoroughly arboreal, tailless, upright-moving, brachiating pro-anthropoid and that the probable time of his first separation from the ancestors of the chimpanzee and the gorilla was hardly earlier than the middle of the Tertiary period.

Even an obstetrician might well be excused if he should mistake this (fig. 1) for a strange sort of human baby. It is Deniker's famous gorilla foetus. The adult gorilla runs on all fours, using its knuckles for supports, but this foetal gorilla is anything but a quadruped. We see at once that the gorilla agrees with man in having the anterior extremity modified into a true hand. Notice also the way the forearm is connected with the body across the broad chest, quite unlike the narrow deep chest of quadrupeds. Its whole general appearance is almost human. A careful comparison of the foetal gorilla with that of man (such as that by Deniker) affords the most cogent evidence that these two forms are relatively closely related in spite of the conspicuous differences in the adults.

Let us turn first to the locomotor apparatus. Here (fig. 2) we see a type of primate that was characteristic of the first half of the Tertiary epoch, one that has

persisted with little modification of the skeleton in certain of the existing lemurs of Madagascar. It was a long-tailed arboreal quadruped with grasping hands and feet, a relatively small brain and eyes that look outward as much as forward. From the construction of its backbone, pelvis and limbs I infer that when this animal leaped or ran it did so after the manner of quadrupeds, with its vertebral

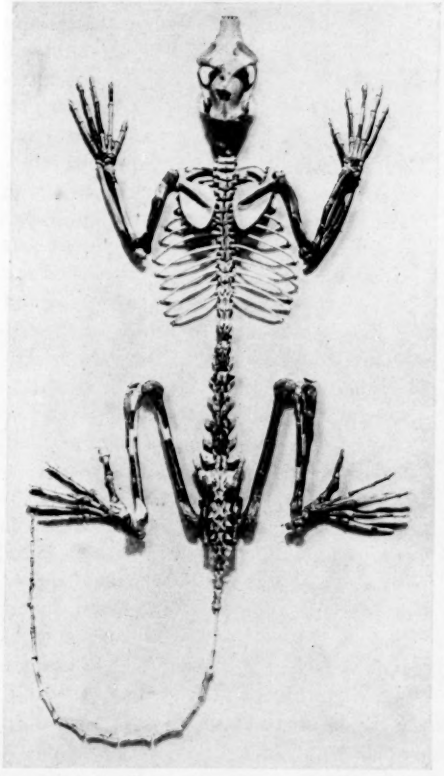

FIG. 2. SKELETON OF *Notharctus osborni*, REPRESENTING A PRIMITIVE STAGE IN THE EVOLUTION OF THE PRIMATES. EOCENE, WYOMING

column nearly horizontal, and from the evident lack of ischial callosities I infer that it did not customarily sit upright as do the monkeys and apes of the Old World.

This animal (fig.3), on the contrary, represents a type of primate that was characteristic of the second half of the Tertiary period, and which from much anatomical and physiological evidence is known to be closely related to the human stem. It no longer holds its body in a horizontal position but at least in sitting and squatting the backbone is rotated upward at 90° to the primitive horizontal

FIG. 3. YOUNG GORILLA IN SQUATTING POSITION
(After Hagenbeck)

position and the head is balanced in this at first difficult position. It is quite tailless, the vestigial caudal vertebrae forming a true coccyx, and some of the former tail muscles have now become enlarged to form a muscular floor of the pelvis. There is even an incipient lumbar curve in the backbone. The eyes are now directed forward and the mouth is below the eyes rather than wholly in front of them. In these and a hundred other significant features this modified survivor of the Mid-Tertiary

anthropoid stock reveals its structural kinship to man. Even the external ear is thoroughly human except in quite minor details.

The adoption of the upright sitting posture and the suspension grasp of a tree-climbing life changed a forefoot into a true hand. Too long continued specialization in this line has changed the orang's hand into a hook, but our own ancestors were driven out of their arboreal paradise before they yielded too far to its transforming spells.

The chimpanzee, it is true, has a hand with a reduced thumb, or rather with unduly elongate fingers, but in view of this figure (fig. 4) by the eminent zoologist J. E. von Boas, can anyone doubt that the chimpanzee has a true hand and that it belongs to a division of the higher primates characterized by having the anterior extremities modified as hands rather than as forefeet?

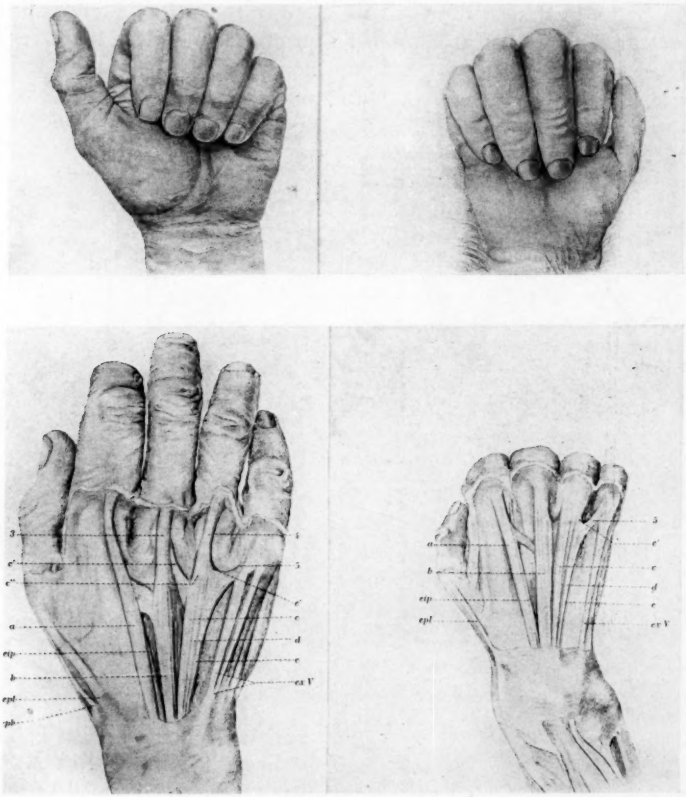

FIG. 4. HAND OF CHIMPANZEE AND OF MAN
(After J. E. von Boas)

And while the chimpanzee thumb may be reduced, all the available evidence forbids us to look for a thumb as

large as this in the remote ancestors of man.

Professor von Boas has also shown that the arrangement of the extensor and flexor tendons in the hand of the chimpanzee is peculiarly human in appearance.

FEET OF APES AND MAN

Turning again to Deniker's gorilla foetus (fig. 5), we see that not only does the gorilla agree with man in having the anterior extremities modified as hands but the hind feet are fundamentally human in structure, differing chiefly in the lesser reduction of the second to the fifth toes and in the divergence of the great toe.

The divergent great toe of the chimpanzee and gorilla has been an occasion of stumbling for the numerous authors that have been unable to see that the human foot is essentially an anthropoid foot with the great toe brought parallel with the others.

This record (fig. 6) of the Mountain Gorilla foot by Akeley has been impugned by Sir Ray Lankester precisely because this foot appeared too human and because he (Lankester) had never seen its like before. But there it stands, and there (fig. 6) is the opposite foot of the same species. In this instance Nature has supplied us with an experimental demonstration of the initial changes necessary to adapt a gorilloid foot in the human direction.

But if the foot of the Mountain Gorilla approaches that of man, the foot of a human foetus of the ninth week, figured by Professor Schultz, assuredly recalls the anthropoid type in so far as its great toe is widely divergent from the others. In the large size of the great toe this foot differs widely in appearance from the foot of primitive Eocene placental mammals other than primates.

An excellent reason for the dominance of the great toe in man, is that in all known primates from the lower Eocene onward the great toe is the anchor or pivot for very strong muscles and tendons of locomotion. The powerful flexors of the great toe aid, even in the oldest primates, in raising the weight of the body, while the great tendon of the peroneus longus muscle was inserted into the strong process on the proximal end of the first metatarsal in all known primates from Eocene lemuroids to man.

FIG. 5. GORILLA FOETUS. SIDE VIEW
(After Deniker)

Hence it seems quite legitimate to infer that when the human foot was made over for use on the ground the same powerful flexor and peroneus muscles of the great toe still served to raise the weight of the body. Moreover, the transverse muscles of the anthropoid foot were used on the ground in preventing collapse of the trans-

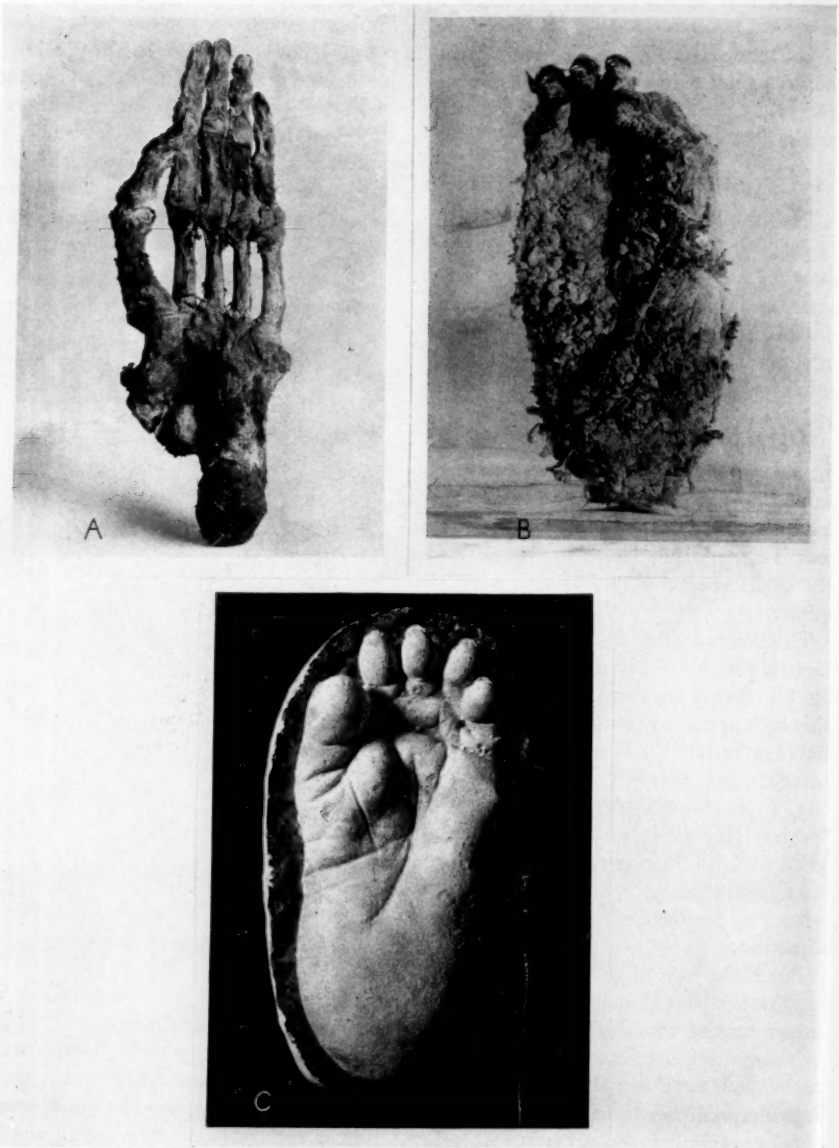

FIG. 6. FOOT OF THE MOUNTAIN GORILLA (GORILLA BERINGEI)
A, skeleton of foot. *B*, right foot after removal of skin. *C*, cast of foot from freshly killed animal, made by the late Carl E. Akeley

verse arch, while the powerful adductor of the hallux assisted in drawing the hallux toward the other digits.

Professor Schultz's researches (1926) on the growth stages of primates have brought strong support to Darwin's view of the close relationship of man to the anthropoid stem. His figure brings out the extraordinary resemblance of the late human foetus to the gorilla. These figures even suggest that man diverged from the gorilla branch after the separation of the chimpanzee and that thereafter the gorilla and man rapidly became extremely different, the former becoming quite secondarily a great-jawed, gigantic quadruped, the latter, a weak-jawed biped. The characters of the brain, ear, etc., are in harmony with this view.

It has been suggested, by myself and others, that some of the characters common to man and one or more of the anthropoids may well be due to "parallelism," that is, to the independent acquisition of similar characters after the divergence from a common stock; but in view of the many positive agreements the burden of proof must rest upon those who would class all of the resemblances as "parallels." In fact, the special resemblances between man and ape, outside of those common to typical mammals, are found in so many different parts of the organism, that the assumption of such extensive parallelism is a mere begging of the question.

STRUCTURAL AND CHRONOLOGICAL KINSHIP

The question, how near is the relationship of man to the chimpanzee-gorilla stock, may be intended in two different senses. We may be thinking either of man's structural kinship, in which case the question may be answered by recounting the degree of resemblance in respect to the different morphological or physiological characters under consideration, or we may be thinking of the degree of kinship in respect to the distance in time back to a common stock and the number of generations since the divergence, along each of the branches. This brings us to the subject of the antiquity of the human family.

Professor Osborn has very forcefully presented the evidence for the existence of

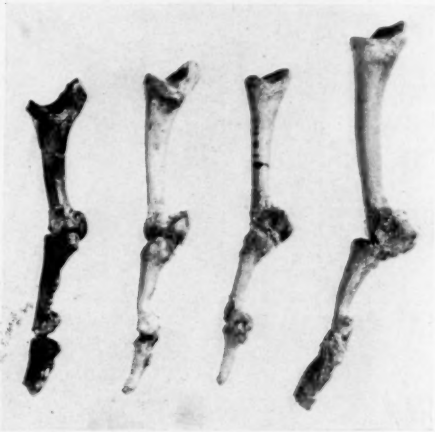

FIG. 7. HALLUX OF FOSSIL AND RECENT PRIMATES, SHOWING PROCESS FOR INSERTION OF TENDON OF PERONEUS LONGUS MUSCLE

A, *Notharctus tyrannus*, Eocene. *B*, *Lemur mongoz*, Recent. *C*, *Cebus capucinus*, Recent. *D*, *Macacus sp.*, Recent

man, as such, in the Pliocene epoch, and he points out that under the newer currently accepted estimates of geologic time man's proved antiquity is at least twenty times greater than it was formerly thought to be.

But in the first place, a good part of this apparent increase is due to the fact that the newer estimates of the length in years of the geologic time epochs are from ten to twenty times longer than the old estimates. Thus the beginning of the Eocene

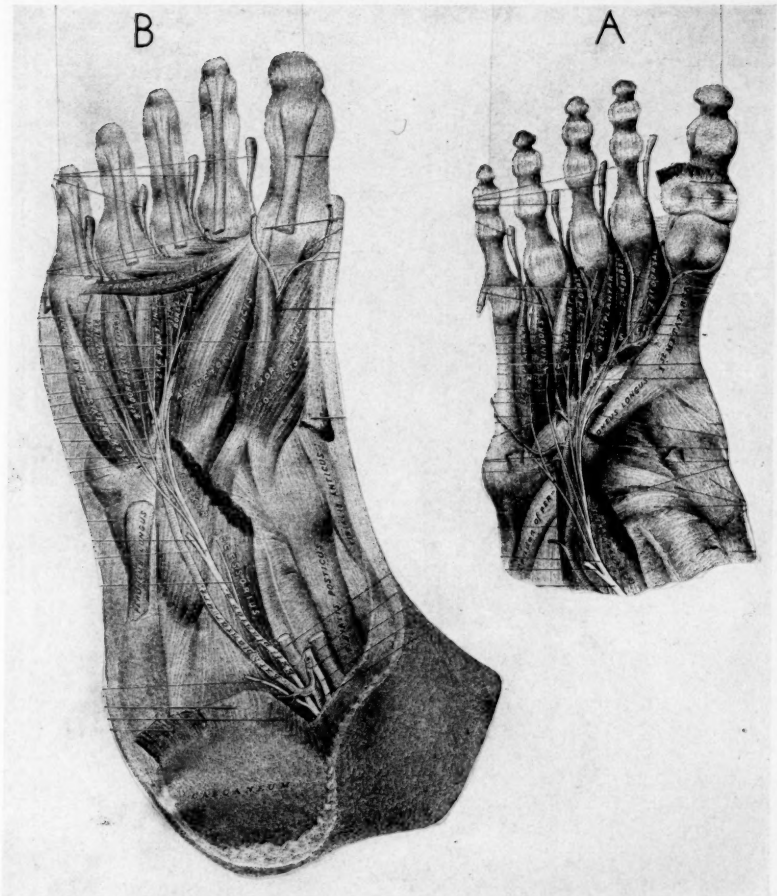

FIG. 8. ANTHROPOID HERITAGE IN THE HUMAN FOOT

A shows insertion of tendon of peroneus longus on proximal end of metatarsal of great toe. *B* shows transversus and flexor hallucis muscles. (After Weisse)

epoch, formerly reckoned as 3,000,000 years ago, is now set back to 60,000,000 years.

Secondly, figure 9 shows that if we accept Barrell's estimates of the length in years of the successive epochs of the Tertiary period, the relative antiquity of the oldest known human fossils as compared with that of various other known fossil primates is as follows:

Man	1 to 3 million years
Dryopithecus	5 to 7 million years
Propliopithecus	33 million years
Eocene Primates	38 to 60 million years

Thus, while the antiquity of man may be twenty times longer than it was formerly

thought to be, yet it is at most only one-twentieth the antiquity of the earliest known fossil primates.

Professor Osborn infers that because some Pliocene horses were almost like modern horses, all Pliocene men were essentially human. Because *Eohippus* had already started on the long road toward *Equus* in the Lower Eocene, the ancestral pro-man already existed in the Oligocene. These deductions, Professor Osborn fervently believes, will be vindicated by future discoveries in Central Asia.

Professor Osborn also believes that because evolution is irreversible no line of apes could ever change into men, since their entire psychology and functions would predestine them to become "super-apes." According to his view, the habit of brachiation which is regarded by Keith and by Gregory as one of the chief prerequisites for both anthropoid and human origin, must lead only to the reduction of the thumb and the transformation of the hands into hooks. But taking a broad view of the animal kingdom, we find not a few instances in which living organisms have broken away from the straight and narrow path of orthogenetic specialization; in new environments they have changed the trend of their evolution and escaped into new evolutionary possibilities. Such radical changes of habitat, as when various lines of marine reptiles and marine mammals were derived from originally terrestrial stocks, always involve profound changes of function. And it is obviously the principle of the change of function which must have been exemplified, no matter from what infra-human source man has been derived.

The myology and osteology of the whole pectoral limb of man constitute a veritable palimpsest, bearing a clearly decipherable record, first, of an earlier period when every bone and muscle was adapted for the habit of supporting the body weight by the uplifted arms, and secondly, of a later stage when the arms were no longer used for locomotion but for the support and manipulation of ob-

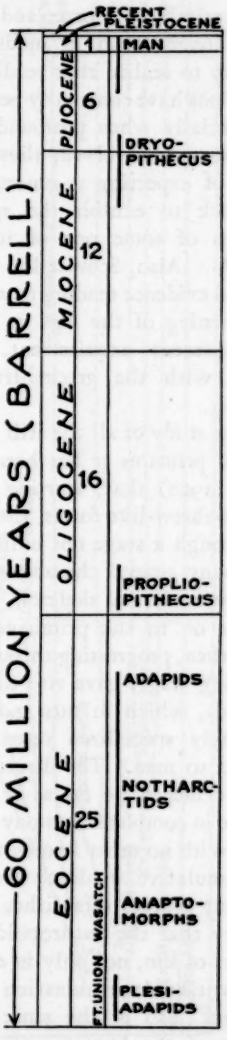

FIG. 9. THE ANTIQUITY OF MAN COMPARED WITH THAT OF OTHER PRIMATES; TIME ESTIMATES (AFTER BARRELL) IN MILLIONS OF YEARS

jects held in the hands. Obviously it is not necessary to infer that in the ancestral anthropoid the extreme specializations for brachiation had already taken place. Great difficulty has been experienced from the fact that in modern man the arms and hands are relatively shorter and the legs relatively longer than in modern apes. This failure to realize that readjustments of proportions have constantly been taking place, especially when profound changes of function were involved, thus leads to the error of expecting a generalized ancestral stock to exhibit the specialized proportions of some one of its remote descendants. Also, Schultz has cited embryological evidence tending to show that the lengthening of the legs in man is a relatively recent acquirement, perhaps correlated with the ground-living cursorial habit.

From the study of all the still surviving families of primates it has been inferred (Gregory, 1920) that, starting from arboreal tree-shrew-like forms, the primates passed through a stage not unlike the lemurs in many general characters, particularly of the brain and skeleton, that they then went on to the primitive monkey stage and then, progressing through an upright sitting stage, gave rise to the pro-anthropoids, which in turn gave rise to the diversely specialized recent anthropoids, and to man. The direct palaeontological evidence, so far as it goes, appears to be in complete harmony with this view and with no other known to me.

The cumulative evidence from many independent sources establishes the high probability that the anthropoid apes are man's next of kin, not only in embryonic development, adult organization and physiology, but also in the sense that the separation of the human and great ape stocks was a far later event in geologic time than the separation of the horse family from the tapir family in the Lower Eocene.

CONCLUSIONS

In brief, I submit the evidence recorded in my previous papers together with the considerations advanced in the present paper, in support of the following conclusions:

I. Considering the evidence afforded by comparative studies on the brains of primates, the anthropoid apes as a whole are undoubtedly man's nearest known relatives, the order of structural relationship being: (1) modernized man; (2) primitive man; (3) gorilla; (4) chimpanzee; (5) orang; (6) gibbon; (7) Old World monkey; (8) New World monkey; (9) *Tarsius;* (10) lemur; (11) pentailed tree-shrew (Elliot Smith, Tilney, Le Gros Clark). Modern students are also convinced that the general order of evolution was the reverse of this, namely, from primitive tree-shrew to lemuroid, to stem tarsioid, to pro-anthropoid, to man.

II. Considering the evidence afforded by the comparative study of the teeth of all known recent and fossil primates, the order of structural evolution is as follows: (1) Generalized tree-shrew (*cf.* Paleocene, *Indrodon*); (2) primitive lemuroid (*cf. Pelycodus ralstoni*, Lower Eocene); (3) primitive tarsioid (*Parapithecus*, Lower Oligocene); (4) proto-anthropoid (*Propliopithecus*, Lower Oligocene); (5) primitive anthropoid (*e.g. Dryopithecus rhenanus*); (6) primitive man (*e.g. Eoanthropus*); (7) modernized man (*Homo sapiens europæus*).

Among existing primates the general order of resemblance to man in the dentition is: (1) chimpanzee; (2) orang; (3) gorilla; (4) gibbon; (5) *Tarsius*.

III. Dr. Gerrit S. Miller and Professor Wood Jones seem to have over-emphasized the fact that the known remains of fossil

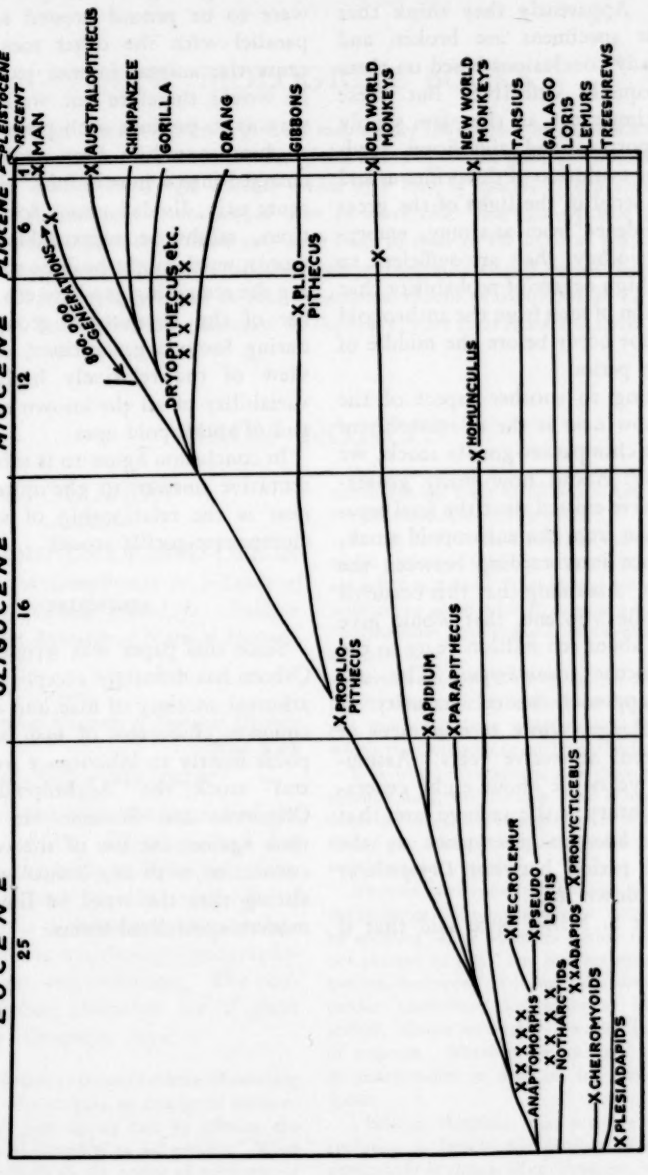

FIG. 10. TENTATIVE PHYLOGENY OF THE PRIMATES

anthropoids consist mostly of broken jaws and teeth. Apparently they think that because the specimens are broken and imperfect, any conclusions based on them must be equally defective. But these specimens, imperfect as they are, supply highly important and significant landmarks in the evolution of the primates and when considered in the light of the great body of evidence from anatomy, embryology, physiology, they are sufficient to establish a high degree of probability that the separation of man from the anthropoid stock did not occur before the middle of the Tertiary period.

IV. Turning to another aspect of the question, how near is the relationship of man to the chimpanzee-gorilla stock, we have to ask: About how many generations may have existed since the final separation of man from the anthropoid stock, that is, since interbreeding between the two ceased. Assuming that this occurred in the Middle Miocene, that would give a period of about ten million years to the Upper Pliocene *Eoanthropus*. The anthropoids approach sexual maturity at ten years of age, while certain races of men can breed at twelve years. Assuming twelve years, or about eight generations to a century as the average rate, that would give 800,000 generations as the transitional period between *Dryopithecus* and the Piltdown man.

Dr. Gerrit S. Miller once said that if the divergent great toe of a chimpanzee were to be pressed around so as to be parallel with the other toes, it would cause the animal intense pain and that he would therefore not walk in such a way as to produce such pressure. Hence a chimpanzee-like foot could never be changed into a human foot. But even an acute pain, divided among 800,000 generations, might be supportable. In other words, much might be done toward bridging the remaining gap between some member of the *Dryopithecus* group and man during 800,000 generations, especially in view of the relatively high structural variability of all the known races of man and of anthropoid apes.

In conclusion figure 10 is submitted as a tentative answer to the question: How near is the relationship of man to the chimpanzee-gorilla stock?

POSTSCRIPT

Since this paper was written Professor Osborn has definitely accepted the remote arboreal ancestry of man and ascribes the common characters of man and anthropoids mostly to inheritance from a "neutral" stock, the "Anthropoidea" of the Oligocene and Eocene. He again protests against the use of the word ape in connection with any human ancestor, insisting that the word be limited to the modern specialized forms.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE DISTRIBUTION OF BIRD-LIFE IN ECUADOR. *A Contribution to a Study of the Origin of Andean Bird-Life. Bulletin of The American Museum of Natural History, Vol. LV, 1926.*

By Frank M. Chapman.

The American Museum of Natural History

$6.00 *New York*

$6\frac{1}{4}$ x $9\frac{1}{4}$; xiii + 784 (paper)

This report embodies the results of ten years work of Dr. Chapman and his assistants on the birds of Ecuador. Like his earlier volume on the bird life of Colombia, it is a monumental contribution to systematic ornithology, geographical distribution, and evolution. The conclusions regarding evolution are of great interest. Dr. Chapman says:

> So I might continue to present evidence illustrating the dependency of evolution on change of environment, but I may sum up my case by offering the entire avifauna of Ecuador as an exhibit. What more adequate tribute to the power of environment can one ask than to discover within this comparatively small but marvelously diversified country one-fourth the birds of all South America and one-twelfth those of the entire world?
>
> In the face of these facts, of the significance of which prolonged field experience has convinced me, I am asked to believe "that chance mutation is quite sufficient to account for all organic evolution," that "environment permits and directs evolution but does not cause it."
>
> Environment, we are told, cannot affect the germ plasm; that its influence therefore is not hereditary; and that only those mutational variations arising within the chromosome can be transmitted.
>
> It is when environment acts through climate or through food, for example, that it apparently produces a change on the organism in which selection has no part, though it must later determine whether such change is desirable.
>
> Whether environment originates or whether, in the language of the day, it merely "starts something" by arousing latent potencies within the germ, I do not pretend to say. But the fact remains that organisms do respond to change and, furthermore, that certain conditions, for example, humidity and aridity, almost invariably provoke the same type of response. Whether the changes are favorable or unfavorable, it remains for environment to decide.
>
> I believe, therefore, that first, as well as last, evolution is largely the product of environment, particularly of change of environment, with its more or less direct action on the organism and its rejection or retention of the resulting characters.

ENVIRONMENT OF THE TETRAPOD LIFE IN THE LATE PALEOZOIC OF REGIONS OTHER THAN NORTH AMERICA. *Carnegie Institution of Washington, Publication No. 375.*
By E. C. Case.
Carnegie Institution of Washington
$2.50 *Washington, D. C.*
9 x 12; iii + 211 (paper)

The final conclusion of this thorough piece of paleontological research is of much interest and significance to biologists in general and geneticists in particular:

> While the author has no suggestion as to the method of evolution, and has no concrete instances to offer in evidence, he is impelled to record here his conviction that the environment is in some way a fundamental factor in the progress. In common with every paleobiologist who has considered evolution in the perspective of time and environment, this conviction is forced upon him. That there are fundamental progressive changes developing independent of the environment through long time, there can be no doubt. That there are series of changes very similar in character, often and consistently repeated, and closely related to synchronously repeated environmental changes, seems equally beyond question. Until the results of the experiments of the neobiologists have stood the test of time, a test which they neglect or sadly undervalue, the author is content to say that, in his opinion, for all adaptive evolutionary changes, the environment either induces the result or acts as the selective screen which determines what forms shall survive and what perish; the environment determines what path life shall take. Whether this statement applies to the major and fundamental changes which have separated the higher groups, even the paleontologist has not as yet the grasp of the effect of time and cosmic environmental changes to venture an opinion.

MIND IN EVOLUTION.
By L. T. Hobhouse. *The Macmillan Co.*
$4.25 *New York*
5½ x 8¾; xix + 483

A reprint, without textual alteration, of the second edition of this standard work. There are added two brief new appendices. The first defends the author's use of the term "correlation" as "at once more general, more plastic, and more significant of mental activity," than the now popular *Gestalt* of the German psychologists. The second new appendix deals with "Instinct in Man," and expands the discussion in the text.

ADAPTIOGENESE UND PHYLOGENESE. *Zur Analyse der Anpassungserscheinungen und Ihrer Entstehung.*
By Albert Eide Parr. *Julius Springer*
Rm. 4.20 6½ x 9½; 60 (paper) *Berlin*

This is the first number of a new series of *Abhandlungen zur Theorie der organischen Entwicklung*, which has been established as a continuation of Roux's *Vorträge und Aufsätze über Entwicklungsmechanik*. The author is of opinion that the genesis of adaptions is a wholly separate phenomenon from phylogenesis, and that there is no need to postulate any adaptive tendency in phylogenesis. The relation of the selection principle to the origination of adaptations is critically discussed. There is no index.

DER ARTENWANDEL AUF INSELN *und Seine Ursachen ermittelt durch Vergleich und Versuch an den Eidechsen der Dalmatinischen Eilande, by Paul Kammerer. Nebst einem Anhang: Zur Systematik der Adriatischen Insel-Eidechsen, by Otto Wettstein.*
Franz Deuticke
30 marks *Leipzig*
6¾ x 10¼; xiv + 324 + 8 plates (paper)

This was Kammerer's last book before his death. It deals exhaustively with variation in the lizards of the Dalmatian islands. Prof. MacBride says (Science Progress, 22: 307) that it "is one of the

finest contributions to the theory of evolution ever written, and deserves to rank with the *Island Life* of Wallace."

GENETICS

VARIABILITÄT UND VARIATION.
By Jur. Philiptschenko.

Gebrüder Borntraeger
5.70 G.M. *Berlin*
6½ x 10; 101 (paper)

The distinguished professor of genetics in the University of Leningrad reviews here the whole question of the different kinds of variation, and attempts to evaluate their significance in evolution. There is little that is novel in the book, but it is a timely, temperate, and well-balanced discussion of a problem of theoretical biology which, as Philiptschenko himself says, cannot possibly be really solved until we have at hand a vastly broader factual basis, especially experimental, than is now available. There is a bibliography of 6 pages, but no index.

GENERAL BIOLOGY

PRINCIPLES OF SOIL MICROBIOLOGY.
By Selman A. Waksman.

The Williams & Wilkins Co.
$10.00 6 x 9; xxviii + 897 *Baltimore*

A colossal piece of text book writing, which has not only technical interest and value for professional soil biologists, but also will be an extremely useful reference work for the general biologist, who has too long completely neglected the fauna and flora of the soil. If he will read this book he will find that a lot of things are going on there which have great theoretical interest. Dr. Waksman is to be congratulated on having produced so thorough and comprehensive a handbook of the field of biology.

THE MIGRATIONS OF BIRDS.
By Alexander Wetmore.

Harvard University Press
$2.50 5 x 7½; viii + 217 *Cambridge*

The material included in this volume constituted a series of Lowell Lectures in Boston. It furnishes a most interesting and valuable review of the present state of knowledge regarding bird migration, one of the most fascinating problems of animal behavior, to the solution of which Dr. Wetmore by his own investigations has contributed much.

EXTRACTS FROM HOOKE'S MICROGRAPHIA. *(First Printed in London in 1665, Reissued by Permission of the Alembic Club of Edinburgh, with Additional Observations on the Cellular Structure of Plants as Revealed for the First Time by the Microscope Constructed by Robert Hooke of Christ Church in Oxford. Old Ashmolean Reprints VI.)*

Old Ashmolean
3 shillings 4¾ x 7½; 60 *Oxford*

This entertaining little reprint of choice bits from the chief work of a versatile genius was prepared as a memento for members of the meeting of the British Association in Oxford in 1926.

DONNÉES NUMÉRIQUES DE BIOLOGIE ET DE PHYSIOLOGIE ET CHIMIE VÉGÉTALES. *Extrait du Volume V, Tables Annuelles de Constantes et Données Numériques.*
By E. F. Terroine and H. Colin (preface by

Léon Fredericq). *Gauthier-Villars et Cie.*
56 francs *Paris*
8½ x 10½; vii + 138 (paper)

Tables of constants, mainly chemical, over a wide and highly scattered series of biological phenomena. It will be found a useful reference work in every biological laboratory.

HUMAN BIOLOGY

TOWARDS THE OPEN. *A Preface to Scientific Humanism.*
By Henry Chester Tracy (with an Introduction by Julian Huxley.) *E. P. Dutton and Co.*
$3.50 5¾ x 8⅝; xx + 257 *New York*

This is a contribution to the philosophy of human biology, by one who is not merely a biologist but has backgrounds—in philosophy, in art, and in humanism generally. While what is said is, by and large, not altogether new, it is extremely well said. Even Faguet never turned a neater one than: "Efficiency exhausts itself in the making of motions by which the illusion of accomplishment is maintained."

The central thesis of the book is that man, by his own stupidity, has taken most of the joy out of living, for all but a relatively few people, and even they have their difficulties in the face of the devastating social inheritance we have managed to load ourselves down with.

"'The open,' towards which we are moving, is a more natural and a freer life in which a man's responsibility is measured by his real relation to his social-natural environment (as shown by the allied sciences bearing on that relation), and his value is measured by his real capacity, discovered under treatment to which he is entitled as a man."

We hope that Mr. Tracy will write some more.

TYPES OF MIND AND BODY.
By E. Miller. *W. W. Norton and Co., Inc.*
$1.00 4¼ x 6½; 95 *New York*

An entertaining brief review of the modern "constitution" theory, so much to the fore just now in medicine. Don Quixote and Sancho Panza serve once more as the paradigmatic asthenic and pyknic respectively; indeed the author dedicates his book to Cervantes with the statement that it is "merely a footnote" to that great man's portraits of these two worthies. Dr. Miller's general position is that: "in order to envisage the whole character of man we must view him, not as body nor as mind, but as an integrated dynamic system of forces which in its inheritance and its own history weaves the fabric of Personality."

This seems sounder doctrine than some we have heard from the constitutionalists.

LA FORCE MOTRICE ANIMALE *à travers les âges.*
By Lefebvre des Noëttes. *Berger-Levrault*
20 francs *Paris*
5½ x 9; viii + 138 + 80 plates (paper)

An interesting piece of archeological and historical research on the evolution of the use of living organisms to furnish motive power to aid man in his enterprises. It is beautifully illustrated with 217 figures on 80 plates. The author distinguishes two periods in the evolution of transportation by animal motive power. In the first man himself was the only efficient motor. In the second period the more effective utilization of animals as sources of motive power freed man from such toil, and paved the way for the

development of mechanical motors. The book is an entertaining contribution to human biology.

A STUDY OF BRITISH GENIUS

By Havelock Ellis. *Houghton Mifflin Co.*
$3.50 5½ x 8¾; xvi + 396 *Boston*

A new edition of a book originally published over twenty years ago. There is no important change from the original form, the author having concluded after deliberation that he cared to make none. There are, however, four new chapters, which follow the "General Conclusions" of the original study. They deal respectively with "The Celtic Spirit in Literature," "The Evolution of Painting in England," "Genius and Stature," and "The Comparative Abilities of the Fair and the Dark." The book is fully documented and indexed. Its reissue in enlarged form is a real service to students of human biology.

OUR EARLY ANCESTORS. *An Introductory Study of Mesolithic, Neolithic, and Copper Age Cultures in Europe and Adjacent Regions.*

By M. C. Burkitt. *The Macmillan Co.*
$2.50 5¼ x 7½; xii + 243 *New York*

A welcome addition to the literature of prehistory, by a master in the field. The overwhelming interest in recent years in paleolithic man and his works has diverted attention from our nearer ancestors of neolithic times. The topical divisions of the subject matter are as follows: mesolithic times; neolithic civilization; typology (of artefacts); neolithic cultures of the eastern area and late neolithic times in central Europe; neolithic cultures of the northern and western areas; England in mesolithic, neolithic, and earliest metal age times; the Mediterranean area and the copper age; bronze age cultures. The book is well illustrated and indexed.

HAIR. *With Special Reference to Hypertrichosis.*

By C. H. Danforth.
American Medical Association
6¾ x 10; 152 *Chicago*

This book is a review of the literature, and of the researches of the author and his colleagues regarding human hair. The topics treated are: The phylogeny of hair; The hair of mammals; General characteristics of human hair; Regional characteristics of human hair; Factors affecting the growth of hair; Aberrant forms of hair growth; Hypertrichosis; General aspects of the hair problem. There is a bibliography covering 7 pages. The work is a valuable contribution to anthropology.

THE RACIAL BASIS OF CIVILIZATION. *A Critique of the Nordic Doctrine.*

By Frank H. Hankins.
Alfred A. Knopf, Inc.
Trade edition $3.75 *New York*
Text edition $2.75
5¼ x 8; xi + 384

The professional Nordics have been encountering very heavy weather of late in their noble voyage to get us safely *into* the trenches of embattled race prejudice by Christmas. Now, in Professor Hankins' book, their ship meets a veritable typhoon. Unless help is rushed to the scene promptly we judge that all of the crew except those who are so oily that surface tension saves them will be *spurlos versenkt*. For Hankins is a rough fellow, and does not spare even Important Persons. We only wish that he had been a little

bit more critically discriminatory in respect of the character of some of the evidence which he accepts as furthering his argument.

GRUNDRISS DER KRIMINAL-BIOLOGIE.

By Adolf Lenz — *Julius Springer*
Reichsmark 15 — *Wien*
6 x 9¼; vii + 252 (paper)

A study of the personality of criminals by the technique of modern "constitution" theory. It is a careful piece of work, well illustrated and documented. Many case histories are presented in considerable detail. The author's position is that a criminal act is to be regarded as the kinetic expression in actuality of a corporeal-spiritual potentiality, which is the total "personality" of the individual, under the influence of the environment. This seems to differ from the average police sergeant's estimate of the nature of criminality only in the nobility of the language in which it is expressed.

BIRTH INJURIES OF THE CENTRAL NERVOUS SYSTEM. *Part I—Cerebral Birth Injuries*, by *Frank R. Ford. Part II—Cord Birth Injuries*, by *Bronson Crothers and Marian C. Putnam.*

The Williams & Wilkins Co.
$4.00 — 6 x 9; xiii + 164 — *Baltimore*

Aside from its considerable obstetrical and psychiatric interest, this volume has a good deal of significance for the thoughtful eugenist. It demonstrates that not a few of the nervous and mental disturbances of later life, which in the normal course of a eugenic investigation get a black mark in the pedigree and are used to elucidate the location of a gene, have nothing whatever to do with genes but are simply expressions of unfortunate obstetric accidents.

RUSSEN UND CHINESEN IN OSTSIBIRIEN.

By Wladimir K. Arsenjew.
August Scherl G. m.b.H.
9.50 gold marks — 6 x 9; 228 — *Berlin*

The Ussur region of Eastern Siberia, bordering the Japanese Sea, has an interesting mixed population of Chinese, Russians, Koreans, and "natives." This interesting volume discusses in considerable detail the economic and social life of this population, with especial reference to their industries. The book is quite extensively illustrated with photographs. Perhaps its greatest interest is for the geographer.

AMERICAN AGRICULTURAL VILLAGES.

By Edmund deS. Brunner, Gwendolyn S. Hughes, and Marjorie Patten (Institute of Social and Religious Research).
George H. Doran Co.
$3.50 — 5½ x 8½; 326 — *New York*

A statistical and sociological study of 140 agricultural villages, ranging in population from 250 to 2500, and scattered over the whole United States, with heaviest incidence of the selection in the eastern part of the country. It continues the two earlier village studies made by the Institute of Social and Religious Research. It is a useful social document, well indexed.

L'HÉRÉDITÉ MUSICALE.

By Louis Vezoux. — *E. le François*
25 francs — 6½ x 10; 279 (paper) — *Paris*

The conclusion of this thesis for the doctorate is that it is heredity alone which makes the musician. Education and the environment merely perfect his talents. There are no new observations, the basis for the conclusions being found chiefly in the writings of American investigators in this field.

CHINA. *A Commercial and Industrial Handbook. Department of Commerce, Bureau of Foreign and Domestic Commerce. Trade Promotion Series No. 38.*
By Julean Arnold, American Consular Officers, and Other Contributors.
Government Printing Office
$1.75 *Washington, D. C.*
5¾ x 9; xvi + 818

No student of the population problem ever gets far in the exhortatory moiety of his lucubrations without dragging in China. While prepared for quite another group of earnest workers this extremely detailed picture of the environmental elements, physical and biological (including social and economic), which operate upon the Chinaman will be found a useful reference source by every student of human biology.

LUTHER BURBANK. *"Our Beloved Infidel." His Religion of Humanity.*
By Frederick W. Clampett.
The Macmillan Co.
$1.50 5 x 7½; 144 *New York*

This is a religious tract, by an Episcopal clergyman, introduced by David Starr Jordan. A perusal of the book leads to the conclusion that Mr. Burbank was an estimable citizen but not a great philosopher.

ZOOLOGY

THE WILD ANIMALS OF AUSTRALASIA. *Embracing the Mammals of New Guinea and the Nearer Pacific Islands.*
By A. S. Le Souef and Harry Burrell, with a Chapter on The Bats of Australia and New Guinea by Ellis Le G. Troughton.
George G. Harrap and Co., Ltd.
25 shillings 5¾ x 9; 388 *London*

The authors of this book have done well a useful thing, in providing in one volume a sound working manual of the mammalian fauna of Australia. About 400 species are included. Brief descriptions are given, with a bibliographical reference to at least one source on the form, necessary keys, and 105 photographic illustrations, besides eight text cuts. In addition there are interesting accounts of the habits and habitats of all the more important forms. The Australasian mammalian fauna is, of course, of extraordinary interest to the student of evolution. In the marsupials nearly every adaptation that is found in any other order of mammals has been independently produced. This book furnishes just what the student of evolution needs—a bird's-eye view of the whole order, which he could get only with great difficulty from the scattered sources in which the different forms have been originally described. The resulting picture is bound to make a profound impression on any thoughtful person, because it presents a gigantic and wholly unsolved problem. This book ought to be in every biological library. The authors are to be congratulated on a fine piece of work.

THE BEAVER. *Its Work and Its Ways.*
By Edward R. Warren.
The Williams & Wilkins Co.
$3.00 5⅜ x 8; xx + 177 *Baltimore*

This second monograph in the series sponsored by the American Society of Mammalogists gives an interesting summary of what is known about the natural history of the beaver, with an abundance of original observations and excellent photographic illustrations. Much current mythology about the super-human intelligence of this remarkable animal is exploded. The residue is, however, sufficiently extraordinary to make one wish that a competent comparative psychologist would devote say ten years time to a real study of the intelligence of the beaver. There is a bibliography and an index.

MONOGRAPH OF THE VOLES AND LEMMINGS (MICROTINÆ) LIVING AND EXTINCT. *Vol. I.*
By Martin A. C. Hinton.
British Museum (Natural History) *London*
30 shillings
5¼ x 8½; xvi + 488 + 15 plates

This is a superb piece of taxonomic work, on an extremely difficult group, upon which the author has been intensively laboring for more than 25 years. A considerable part of the difficulty arises from the fact that in many of the Microtinæ, and especially the genus *Arvicola*, "apparently, that is so far as actual observation goes, voles of this genus are animals that never stop growing and never grow old." Fossil as well as living species are described. The first 136 pages are devoted to a masterly discussion of the structure and evolution of the group. The remainder contains an extremely thorough and critical systematic account of the 31 genera of Microtinæ, of which 14 are here revised. The volume has great interest for the student of evolution as well as for the systematic mammalogist.

MEDICAL REPORT OF THE HAMILTON RICE SEVENTH EXPEDITION TO THE AMAZON, IN CONJUNCTION WITH THE DEPARTMENT OF TROPICAL MEDICINE OF HARVARD UNIVERSITY, 1924–1925. *Contributions from the Harvard Institute for Tropical Biology and Medicine, No. IV.*
By Richard P. Strong, George C. Shattuck, Joseph C. Bequaert, and Ralph E. Wheeler.
Harvard University Press
$4.00 7½ x 10½; xvi + 313 *Cambridge*

The first part of this extensively and beautifully illustrated report, by R. P. Strong, G. C. Shattuck, and R. E. Wheeler, deals with the results of the investigation of various tropical diseases. The second part, by J. Bequaert, is concerned with medical and economic entomology, while the third part is a miscellany of geographical, medical, and zoological investigations, contributed to by G. C. Shattuck, J. H. Sandground, and J. Bequaert. The whole report makes a valuable contribution to tropical biology and medicine.

BIOLOGIE DER HYMENOPTEREN. *Eine Naturgeschichte der Hautflügler.*
By H. Bischoff. *Julius Springer*
Reichsmark 27 *Berlin*
6¼ x 9½; vii + 598 (paper)

We have already noticed in these pages earlier volumes in the series of *Biologische Studienbücher*, of which the present book is the fifth number. It is a comprehensive review of the biology of hymenopterous insects. The topics treated are: structure; taxonomy; phylogeny; distribution; movement; nutrition; respiration and circulation; nervous system; nests; eggs and egg laying; brood husbandry; parasitism; social life; sex life; development; adaptation; diseases. There is a bibliography

of 12 pages, and detailed indices. Altogether Dr. Bischoff has given us a valuable reference work.

DELINEATIONS OF AMERICAN SCENERY AND CHARACTER.
By John James Audubon.
Simpkin, Marshall, Hamilton, Kent and Co.
$4.50 6 x 9¼; xlix + 349 *London*

In this book are collected for the first time in a single volume, and in modern (and excellent) typographical dress, the essays which Audubon interspersed between the plates, in his *Ornithological Biography*, under the titles of "Episodes" or "Delineations of American Scenery and Character." There is a sympathetic, though critical, estimate of Audubon's life and work by Professor Francis Hobart Herrick as an introduction. The whole is a useful addition to the literature of biological history. Unfortunately there is no index, which greatly impairs the usefulness to the student of a book of this character.

LE COMMUNISME CHEZ LES INSECTES.
By E.-L. Bouvier. *Ernest Flammarion*
13 francs 4¾ x 7⅞; 291 (paper) *Paris*

A discussion of the biology of social insects, having for its object the discovery of the spirit which animates such societies. The general conclusion reached is that insect societies are, like human societies, the expression of two kinds of psychological forces, the first instinctive, to which each individual responds blindly, the second plastic and more or less intelligent, permitting the individual to have some initiative in adapting his acts to the circumstances.

THE ELEMENTS OF GENERAL ZOOLOGY. *A Guide to the Study of Animal Biology Correlating Function and Structure, with Notes on Practical Exercises.*
By William J. Dakin.
Oxford University Press
$4.00 5½ x 8½; xvi + 496 *New York*

In this elementary textbook emphasis is laid primarily upon function rather than structure. This method of teaching the subject is apparently more novel, at the moment, in England than it is with us. Laboratory directions are incorporated in the text. American teachers can get some helpful suggestions from the book.

ÜBER GRENZEN DES WACHSTUMS.
By Richard Hesse. *Gustav Fischer*
Mk. 2 6⅜ x 9¼; 36 (paper) *Jena*

A detailed presentation of comparative anatomical evidence in support of the argument that the body size of an animal is a function (in the mathematical sense) of the area of the epithelial surface of the intestine. Most of the data relate to invertebrates. The author does not overlook the fact that other factors are concerned in the determination of body size.

FAUNE CAVERNICOLE DE LA FRANCE. *Avec une Étude des Conditions d'Existence dans le Domaine Souterrain.*
By René Jeannel. *Paul Lechevalier*
75 francs 6½ x 10; 334 (paper) *Paris*

This part of *Encyclopédie Entomologique* is a fine piece of ecological work on cave faunas. The first section, dealing with general ecological conditions and faunal relations in caverns, is followed by a detailed taxonomic list of the invertebrate fauna of French caves.

BOTANY

MANUAL OF CULTIVATED TREES AND SHRUBS HARDY IN NORTH AMERICA. *Exclusive of the Subtropical and Warmer Temperate Regions.*
By Alfred Rehder. *The Macmillan Co.*
$10.50 *New York*
5½ x 8½; xxxvii + 930

This book gives detailed taxonomic descriptions of over 2500 species (with their varieties) of cultivated trees and shrubs, in which category are included also woody vines, bamboos, cacti, and suffruticose plants. It is intended to serve the same purpose as Gray's Manual in the field covered. The work is extremely well done, and should long serve as a valuable reference work, not only to professional botanists, but to gardeners, nurserymen, and tree lovers generally.

ÖKOLOGIE DER ASSIMILIERENDEN HÖHLENPFLANZEN.
By Friedrich Morton.
Urban und Schwarzenberg
6 marks *Berlin*
6¾ x 9½; 84 + 3 plates (paper)

This is a worthy companion on the botanical side to the French treatise on cave fauna, noticed elsewhere in this issue of THE QUARTERLY REVIEW OF BIOLOGY. The adaptations, both morphological and physiological, of plants to cave life are extraordinarily interesting. There is a selected bibliography covering 7 pages.

BIOLOGIE DE LA CELLULE. ÉVOLUTION DES CHROMATINES. *Leurs rapports entre elles et avec la cinèse. 1. Dans le tige aérienne de l'Equisetum arvense L. 2. Dans le sac embryonnaire du Fritillaria imperialis L. (Divisions I et II).*
By Maurice Lenoir. *Gaston Doin et Cie.*
55 francs 6½ x 10; 207 (paper) *Paris*

The subject matter of this cytological investigation, which constitutes *Fasciule 26* of the *Archives de Morphologie Générale et Expérimentale*, is sufficiently indicated by the title.

ÜBER KÜNSTLICHE BLATT- UND BLÜTENMETAMORPHOSEN BEI DER SCHNEEBEERE (*Symph. rac. Michx.*) (*Nebst Versuch einer charakterologischen Analyse pflanzlicher Lebensfunktionen*).
By Hans André. *Gebrüder Borntraeger*
10.50 marks *Berlin*
6½ x 10; vii + 125 + 2 plates

An interesting contribution to the physiological morphology of *Symphoricarpus racemosus*.

OBSERVATIONS ON THE GRASSLANDS OF THE CENTRAL UNITED STATES. *Ohio State University Studies. Contributions in Botany No. 178.*
By John H. Schaffner.
Ohio State University Press
$1.25 6½ x 10; 56 (paper) *Columbus*

An ecological study.

SOIL CONDITIONS AND PLANT GROWTH.
By Edward J. Russell.
Longmans, Green and Co.
$6.50 5¼ x 8½; viii + 516 *New York*

The fifth edition of what has now become an agricultural classic. Owing to the rapid advancement of the subject since 1921 it has been necessary to rewrite all except the historical portions of the

book. It is, in its present form, a work of great general biological interest, as well as a standard reference text for the agriculturist.

POSSIBILITIES FOR PARA RUBBER PRODUCTION IN NORTHERN TROPICAL AMERICA. *Department of Commerce, Bureau of Foreign and Domestic Commerce. Trade Promotion Series No. 40.*
By John C. Treadwell, C. Reed Hill, and H. H. Bennett. *Government Printing Office*
65 cents *Washington, D. C.*
5¾ x 9¼; xii + 375 (paper)

An interesting contribution to applied ecology, which no botanical library should lack, considering its very moderate price.

MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. *Vol. XVIII, Nos. 90 to 97. (Publication No. 363). No. 90. Cultivation of Embryonic Heart-Muscle, by Warren H. Lewis. No. 91. Correlation of External Genitalia and Sex-Glands in the Human Embryo, by Karl M. Wilson. No. 92. The "Miller" Ovum —the Youngest Normal Human Embryo thus far Known, by George L. Streeter. No. 93. Detailed Form of the Wolffian Body in Human Embryos of the First Eight Weeks, by Jujiro Shikinami. No. 94. Lens Ectoderm and Optic Vesicles in Allantois Grafts, by Vera Danchakoff. No. 95. Menstrual Records and Vaginal Smears in a Selected Group of Normal Women, by Jessie L. King. No. 96. Transformation of Mononuclear Blood-Cells into Macrophages, Epithelioid Cells in Hanging-Drop Blood Cultures from Lower Vertebrates, by Margaret R. Lewis and Warren H. Lewis. No. 97. Origin of Thrombocytes and of the Different Types of Blood-Cells as Seen in the Living Chick Blastoderm, by S. Sugiyama.*
Carnegie Institution of Washington
$5.75 *Washington, D. C.*
9¼ x 11½; 148 (paper)

This volume, with its beautiful plates, well maintains the high standard to which we are accustomed in the output of the Department of Embryology of the Carnegie Institution. Papers No. 90, 91, 92, 94, 95, and 96 are of noteworthy *general* biological interest. Perhaps the most important discovery recorded in the volume is that of the Lewis family (Paper No. 96) to the effect:

"(1) That the mononuclears, macrophages, and epithelioid cells are merely different phases of the same cell type.

"(2) That the transformation of the mononuclears into macrophages, epithelioid cells, and transition forms can scarcely be considered as a true differentiation into new and fixed types of cells.

"(3) That these different forms are more in the nature of temporary functional variations of the same cell type."

ANATOMICAL TEXTS OF THE EARLIER MIDDLE AGES. *A Study in the Transmission of Culture. With a Revised Latin Text of Anatomia Cophonis and Translations of Four Texts. Carnegie Institution of Washington Publication No. 364.*
By George W. Corner.
Carnegie Institution of Washington
$1.00 *Washington, D. C.*
6¾ x 10; 112 (paper)

Professor Corner has not hitherto been known as a medical historian, but this volume will firmly establish his reputation in that field. It is a thorough piece of work, intelligently conceived and critically carried out, and is an important contribution to the history of science, quite

beyond its value in the narrower field of medical history. There has long been an argument as to whether the trained scientific worker could write the history of science better than the trained historian who decided to choose the history of science as his particular field of research. Dr. Corner's book furnishes heavy ammunition for those who take the former position.

THE SPINY DOGFISH. *A Laboratory Guide.*
By Alvin R. Cahn. *The Macmillan Co.*
$1.10 $4\frac{3}{4}$ x $7\frac{1}{2}$; xii + 94 *New York*

THE SKATE, *Raja erinacea Mitchill. A Laboratory Manual.*
By Charles W. Creaser. *The Macmillan Co.*
90 cents $4\frac{3}{4}$ x $7\frac{1}{2}$; x + 57 *New York*

NECTURUS. *A Laboratory Manual.*
By L. A. Adams. *The Macmillan Co.*
$1.00 $4\frac{3}{4}$ x $7\frac{1}{2}$; vii + 72 *New York*

These three laboratory guides for the dissection of lower vertebrates, widely used in class work in comparative anatomy, follow traditional lines.

VARIATIONS IN THE FORM OF THE JAWS. *With Special Reference to Their Etiology and Their Relation to the Occlusion of the Dental Arches.*
By J. Sim Wallace. *William Wood and Co.*
$6.00 $6\frac{1}{4}$ x $9\frac{1}{2}$; xii + 265 *New York*

It is wonderful to observe the growth of specialism in science. Probably no branch of the practice of medicine has, on the whole, been more expressive of the spirit of a technical art, and less animated by what we like to think of as the real soul of science, than has dentistry. But times change. Here is a scientific analysis of one of the categories of biological phenomena which make trouble for dentists. The anatomist will find it a stimulating and useful book. It received the Cartwright Prize.

A SYNOPSIS OF THE GENERAL MORPHOLOGY OF ANIMALS.
By Edwin Grant Conklin.
Princeton University Press
$1.50 *Princeton, N. J.*
$5\frac{3}{4}$ x $8\frac{1}{2}$; ix + 85

A masterly presentation of the broad facts and principles of animal morphology, with extreme conciseness and clarity. We know of no book in the whole literature of zoology which does so well what this one accomplishes in so little space.

PHYSIOLOGY

MÉTABOLISME DE L'EAU. *Œdèmes—Diurèse—Les Thérapeutiques Hydriques.*
By Marcel Labbé and P.-L. Violle.
Masson et Cie.
28 francs 6 x 9; 256 (paper) *Paris*

This is an excellent presentation of the French point of view in regard to the physical and chemical conditions that determine the amount of water held in the tissues at any one time, and as such it will be of value to the many who are now becoming interested in this highly important branch of biochemistry. One only regrets that, like so many of their countrymen, the authors either ignore or belittle the many contributions to the subject made by investigators in Germany, England, and America. One wonders sometimes whether this sort of thing is done mainly because a writer is not willing to take the word of a foreigner or to give him credit, or because he cannot read any language but his own.

TEXTBOOK OF COMPARATIVE PHYSIOLOGY.
By Charles Gardner Rogers.
McGraw-Hill Book Co., Inc.
$5.50 5¾ x 9; xvi + 635 *New York*

A useful textbook of general physiology on a comparative basis. There is a bibliography of 30 pages and a detailed index. The book is well illustrated and constitutes a valuable addition to the text book literature of general biology.

L'EXCITABILITÉ EN FONCTION DU TEMPS. *La Chronaxie, sa signification et sa mesure.*
By Louis Lapicque.
Les Presses Universitaires de France
45 francs 6 x 9½; 371 *Paris*

A critical review, by the professor of general physiology at the Sorbonne, of the present state of knowledge regarding the time relations in the response to stimuli of a nerve-muscle preparation. The treatment is extremely thorough, from the historical, experimental, theoretical, and methodological standpoints. There is a bibliography covering five pages.

GLYCOGÉNE, ADRÉNALINE ET INSULINE.
By M. Jacot. *Masson et Cie.*
35 francs 6 x 9; 210 (paper) *Paris*

This is a readable discussion of some experiments designed to show the physico-chemical relationships between glycogen, adrenalin, and insulin. They started from the observations (1), that adrenalin when added to a sol of glycogen will reduce the size of the particles and will remove the turbidity; (2), that glycogen acts on adrenalins as an oxidizing agent; and (3), that insulin has a tendency to flocculate glycogen.

Unfortunately, like many other men who come forward with interesting observations and theories, Jacot largely ignores what others have done on his problem; he fails to place his contribution in its proper relation to all that has gone before, and he leaves all but his most highly specialized readers wondering whether they have heard something new or something already disproved.

PHYSIK UND CHEMIE DES RADIUM UND MESOTHOR. *Für Ärzte und Studierende.*
By Albert Fernau. *Julius Springer*
Rm. 7.50 *Wien*
6 x 9; v + 101 (paper)

The second edition of a useful elementary text on the biophysics of radioactive substances. The treatment is very concise, but clear, and the information is presented with a minimum of mathematics. There is a short bibliography appended, but no index.

THE SCIENTIFIC FEEDING OF ANIMALS.
By O. Kellner (Authorized translation by William Goodwin).
Gerald Duckworth and Co.
8 s. 6 d. 4¾ x 7¼; xiii + 328 *London*

A second English edition of a well-known, standard text in the field of animal nutrition. A chapter on vitamins and a fuller discussion of the making of silage are the most important additions.

BEWEGUNGEN UND INNERVATION DES WIEDERKÄUERMAGENS.
By E. Mangold and W. Klein.
Georg Thieme
3.60 marks 6¾ x 10; 58 (paper) *Leipzig*

An interesting experimental contribution to the physiology of the vegetative nervous system.

BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 218.* FERMENTFORSCHUNG. *Containing following articles: Darstellung polypeptidspaltender Fermentsole aus Hefe und Pankreas, by Andor Fodor and A. Bernfeld; Esterasen, by Peter Rona; Carboxylase, by Carl Neuberg; Sulfatase, by Carl Neuberg and Joachim Wagner; Abfangverfahren, by Carl Neuberg and Maria Kobel; Phosphatasen, by Carl Neuberg and Ernst Simon; Carboligase, by Carl Neuberg and Maria Kobel; Phytochemische Reduktionen, by Carl Neuberg and Günther Gorr; Die Methylenblaumethode zum Studium der biologischen Oxydationen, by Gunnar Ahlgren.*

Urban und Schwarzenberg
Mk. 9 7 x 10; 187 (paper) *Berlin*

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 220. Methoden der mikrobiologischen Bodenforschung.*
By Selman A. Waksman.
Urban und Schwarzenberg
Mk. 7.20 7 x 10; 150 (paper) *Berlin*

The first of these two numbers of the Abderhalden handbook appeals only to workers in rather restricted special fields of biology, but Dr. Waksman's contribution, which is a very thorough exposition of the technique of soil microbiology, has possibilities of interest to the general biologist, who has, generally speaking, rather neglected the possibilities of the soil to furnish useful material for laboratory investigations.

SULFUR METABOLISM. *A Review of the Literature.*
By Max Kahn and Frederic G. Goodridge.
Lea and Febiger
$9.00 *Philadelphia*
$5\frac{3}{4}$ x $9\frac{1}{4}$; xiv + 831

This solid, substantial reference work fittingly serves, as the authors suggest in the preface, to complete the trilogy of review treatises on metabolism, which began with Atwater and Langworthy's *Digest of Metabolism Experiments*, followed many years later by Forbes and Keith's *Phosphorus Compounds in Animal Metabolism.* The compilation of this volume on sulphur was obviously a colossal task. But the authors will have the blessing of students for a long time to come. The thoroughness of the treatment is evident in the first chapter. It includes 135 pages and is devoted to the literature on the sulphur content of the various organs, tissues, and fluids of the body, exclusive of the urine.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *In 75 Vorlesungen, für Studierende, Ärzte, Biologen und Chemiker. I. Band: Organchemie. III. Lieferung: Organe mit Innerer Sekretion, Geschwülste. Vorlesung: XXX bis XL.*
By Otto Fürth. *F. C. W. Vogel*
Marks 15 *Leipzig*
7 x 10; v + 166 (paper)

This part of the Fürth textbook, earlier portions of which have been previously noticed in THE QUARTERLY REVIEW OF BIOLOGY, is of particular interest to the general biologist, because it includes a discussion of the biochemistry of the sex organs and of embryonic development, along with the treatment of other organs of internal secretion.

THE DETERMINATION OF HYDROGEN IONS. *An Elementary Treatise on the Hydrogen Electrode, Indicator and Supplementary Methods with an Index Bibliography on Applications.*
By W. Mansfield Clark.
The Williams & Wilkins Co.
$5.00 6 x 9; 480 *Baltimore*

This second edition of the standard American text on hydrogen ion technique has been considerably rewritten and brought up to date. Nine hundred new titles have been added to the bibliography, bringing the total up to over 2000.

LEITFADEN FÜR BIOCHEMISCHE MIKROMETHODEN. *Als Laboratoriumsbuch zusammengestellt für das Biochemische Laboratorium der Vereinigten Fabriken für Laboratoriumsbedarf von deren wissenschaftlichem Beirat.*
By Paul Ruszczynski.
Vereinigten Fabriken für Laboratoriumsbedarf Ges. m. b. H.
Reichsmark 3 7 x 10; 163 *Berlin*

An apparatus catalogue, annotated to show how the apparatus is to be used. This is a good idea, which might profitably be extended to other fields than biochemical micro-technique.

SEX

SEX FREEDOM AND SOCIAL CONTROL.
By Charles W. Margold.
The University of Chicago Press
$2.00 $5\frac{1}{4}$ x $7\frac{5}{8}$; xi + 143 *Chicago*

This book attacks one of the main roots of birth-control philosophy. Its principal thesis is that the "distinction between sexual relations that result in offspring—and therefore held as social—and sexual relations that do not result in procreation—and therefore urged as individual—is not sound."

It is concluded, after a very heavily documented sociological and anthropological discussion (the bibliography runs to 486 titles) that "due to the special importance of sex matters in man's life, individuals and groups can, as a matter of conscious planning, relinquish the intentional or higher-control phases in sex, only at their peril. They neglect the purposive safekeeping, from generation to generation, of the social heritage in regard to sex conduct, only at their own undoing. It seems probable, therefore, as to the future, that social control will continue, even on its more organized levels, purposively to institute group modes of sex conduct, and to insist upon them when necessary, together with other means, also through legislative enactment and state enforcement."

We greatly fear that the whole tenor of this treatise is counter to the philosophy of the "youth" movement which seems the most striking social phenomenon of the present time all over the world. And it must be confessed that the last clause of the last sentence quoted has an ominous sound. Reginald, our office boy, offered to bet the janitor 6 to 5 that Professor Margold is an active, due-paying member of the Anti-Saloon League, but fortunately this shocking proposal was overheard and both malefactors were disciplined.

CONTRE FREUD. *Critique de Toute Psychologie de l'Inconscient.*
By Jean Bodin. *Masson et Cie.*
14 francs *Paris*
$6\frac{1}{2}$ x $9\frac{3}{4}$; iv + 99 (paper)

A treatise preliminary to a larger work

on personality. In preparing this the author found it desirable to clear the ground of prior, and in his opinion, unsound theories. Hence this volume, which is a detailed critique of Freud, in some points penetrating and sound.

DIE WIRKUNGSWEISE ABGESTUFTER KEIMDRÜSENSCHÄDIGUNG. *Eine experimentelle Studie zur Frage der endokrinen Sexualfunktion.*
By Heinrich Viktor Klein.
Urban und Schwarzenberg
Marks 12 *Berlin*
7 x 10; vi + 144 (paper)

After a review of the literature covering 80 pages the author gives an excellent account of his own experiments on guinea pigs and rabbits, involving castration, autoplastic transplantation of gonads, ligature of the vas deferens, X-ray radiation of the gonads, and partial removal of radiated gonads. The conclusions from what seems to have been a careful and critical piece of work are extremely interesting, but too voluminous to present here. One point only may be noted: neither ligation of the vas nor X-ray radiation of the gonads produced any constant, marked, or permanent increase in interstitial cells.

BIOMETRY

DAS EXPONENTIALGESETZ ALS GRUNDLAGE EINER VERGLEICHENDEN BIOLOGIE.
By Ernst Janisch. *Julius Springer*
Reichsmark 28.20 *Berlin*
$6\frac{1}{4}$ x $9\frac{1}{2}$; iv + 383 (paper)

An enormously painstaking review of the great range of biological phenomena which, in whole or in part, and in greater or smaller degree, follow the law of compound interest in their quantitative relations, in one or another of its forms. There is a bibliography covering some 10 pages. The book will be a useful reference source in any biological research laboratory.

PSYCHOLOGY AND BEHAVIOR

THE MEASUREMENT OF INTELLIGENCE.
By Edward L. Thorndike, E. O. Bregman, M. V. Cobb, Ella Woodyard, and the Staff of the Division of Psychology of the Institute of Educational Research of Teachers College, Columbia University.
Teachers College, Columbia Univ.
$4.00 6 x 9; xxvi + 616 *New York*

The position of the authors is that: "An intellectual task is one, success in which depends upon all of intellect and nothing but intellect. Intellect is definable by a series of tasks, and we have so defined one variety of it, Intellect CAVD, and could so define any other variety of it. A CAVD intellectual task is, then, one success at which depends upon all of Intellect CAVD and nothing but Intellect CAVD. Tasks can be devised which do substantially meet this requirement, success at one of them correlating perfectly (or as closely as its own self-correlation permits) with success in the entire series."

The tasks upon which intellect CAVD is defined are:

"C. To supply words so as to make a sentence true and sensible.

"A. To solve arithmetical problems.

"V. To understand single words.

"D. To understand connected discourse as in oral directions or paragraph reading."

The book is a detailed technical account of an extensive investigation of intellect CAVD. Its significance at this stage of the development of the subject seems to be chiefly methodological.

THE FATHER IN PRIMITIVE PSYCHOLOGY.

By Bronislaw Malinowski.

W. W. Norton and Co., Inc.

$1.00 4¼ x 6½; 95 *New York*

This little book is a joy. Written with consummate skill and deep knowledge, it describes the psychology of the natives of the Trobriand Islands regarding the physiology of human and animal reproduction, and the social consequences which flow from their incomplete knowledge of this subject. They believe that the male has no significant physiological part in reproduction, and the cogency of the arguments with which they support this view is a delight. This doctrine is basically embodied in their whole social organization. Perhaps the most entertaining thing about it all is that by every pragmatic test the whole system works just as well, though founded on this plain biological error, as do systems founded on its truthful antithesis. One is tempted to enquire about the price of pragmatism, considered as a test of "truth."

THE NATURAL HISTORY OF OUR CONDUCT.

By William E. Ritter, with the collaboration of Edna Watson Bailey.

Harcourt, Brace and Co.

$3.50 5¾ x 8½; ix + 339 *New York*

Anything that Professor Ritter writes is sure to be interesting and provocative of thought. The latest volume is no exception. It is an extraordinarily entertaining attempt at a consistent exposition of what might perhaps be called phylogenetic behaviorism. Applying essentially that type of reasoning which was characteristic of the good old science of comparative morphology, with of course intelligent modifications suitable to the nature of the subject, the author brings together a mass of evidence showing how the activities of lower animals form a graded series which can be interpreted as steps in an evolutionary process which culminates in human behavior. However much one may disagree with details of its conclusions or its philosophy, this is a stimulating book, well worth the attention of every biologist. It includes a bibliography of four pages, and a detailed index.

THE MIND AND ITS MECHANISM. *With Special Reference to Ideo-Motor Action, Hypnosis, Habit and Instinct, and the Lamarckian Theory of Evolution.*

By Paul Bousfield and W. R. Bousfield.

E. P. Dutton and Co.

$4.00 5½ x 8½; vii + 224 *New York*

This book sets forth a novel scheme for bridging the psychophysical gap. The authors postulate a new kind of matter, which somewhat paradoxically is stated to be "immaterial." It is composed of "psychons" which are like electrons except that they are different. The psychons make up a "psychic brain" which implements the *liaison* between consciousness and the nervous system. Space lacks for a complete exposition of the theory here. It is undeniably ingenious, but beyond this there seems little to recommend it.

A SHORT OUTLINE OF COMPARATIVE PSYCHOLOGY.
By C. J. Warden.
W. W. Norton and Co., Inc.
$1.00 4¼ x 6½; 96 *New York*

This is a brief history of thought and work on animal behavior, well written, and with penetrating insight. While issued in a popular series, this volume is well worth the attention of serious students.

AN INTRODUCTION TO THE THEORY OF PERCEPTION.
By Sir John Herbert Parsons.
The Macmillan Co.
$5.25 6 x 9½; 254 *New York*

A thorough, critical review, with extensive documentation, of the present state of knowledge of the physiological psychology of man's sense organs. It tells what is known of the biological mechanisms by which man becomes aware of his environment.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE LOGIC OF MODERN PHYSICS.
By P. W. Bridgman.
The Macmillan Co.
$2.50 6 x 8¾; xiv + 228 *New York*

This seems to us to be a great book. Physics is just now in the midst of a period of uninhibited theorizing which has many of the objective attributes of a drunken party. The joys of inebriety are notorious, but unfortunately experience teaches that there is always a "morning after." To remind his colleagues in the domain of physics of this hard and disagreeable fact was, we take it, Professor Bridgman's main object in writing this book. Its philosophical significance, however, is much broader than the science of physics. The biologist, and especially the geneticist, will do well to read and ponder over it.

Dr. Bridgman is an experimentalist of the very first rank. There are very few physicists living who can equal or surpass his record as an experimentalist. The importance of this book lies in the fact that such a man turns a cold, shrewd, and perhaps even slightly bilious eye upon the fundamental concepts of his science, at a time when they are being subjected to a considerable revision every other Tuesday.

It is impossible to do justice to the book in the space that can be devoted to it. Really all we can do is to recommend biologists *to read it*. And that we do most earnestly. It is not precisely easy reading, but this is only because the argumentation is everywhere closely knit, not because of heavy mathematics or other technicalities. The key note of the philosophy of the book is that knowing is doing *et praeterea nihil*.

> What do we mean by the length of an object? We evidently know what we mean by length if we can tell what the length of any and every object is, and for the physicist nothing more is required. To find the length of an object, we have to perform certain physical operations. The concept of length is therefore fixed when the operations by which length is measured are fixed: that is, the concept of length involves as much as and nothing more than the set of operations by which length is determined. In general, we mean by any concept nothing more than a set of operations; *the concept is synonymous with the corresponding set of operations*. If the concept is physical, as of length, the operations are actual physical operations, namely, those by which length is measured; or if the concept is mental, as of mathematical continuity, the operations are mental operations, namely those by which we determine whether a given aggregate of magnitudes is continuous.

This has a refreshing sound, and there is a great deal more of the same invigorating medicine in the book. Read it!

LES CANCERS DU SEIN.
By Pierre Delbet and Mendaro.
Masson et Cie.
50 francs 6½ x 10; 343 (paper) *Paris*

LES CANCERS ET LEURS COMPLICATIONS. *Étude Clinique de Leur Évolution.*
By Maurice Renaud. *Masson et Cie.*
30 francs 6 x 9¼; 322 (paper) *Paris*

DIAGNOSTIC DES PRINCIPAUX CANCERS.
By Henri Hartmann (with the collaboration of Mm. Bensaude, Bérard, Chevassu, Darier, Forgie, Legueu, Lemaitre, Michon, Morax, Nové-Josserand, Okinczyc, Rist, Roussy, Sébileau). *Masson et Cie.*
10 francs 6 x 8¾; 64 (paper) *Paris*

These volumes concern the medical man rather than the general biologist. All three are eminently practical treatises written with the precision of style for which good French writing is so justly famed. The first two are extensively and well illustrated.

A PSYCHOLOGICAL STUDY OF CANCER.
By Elida Evans. *Dodd, Mead and Co.*
$2.50 5½ x 8; viii + 226 *New York*

Psychoanalysts are going to have a lot of answering to do when they are lined up before the Judgment Seat. The author of this treatise is a pupil and follower of Jung. She has psychoanalyzed a number of cancerous persons. From this experience she has generalized, with the results exhibited in this book. It seems that cancer patients are "feeling extraverts, full of life and activity." "That part of the body attacked [by cancer] we have found to have been the seat of the detached libido. In women it is most frequently the maternal organs, as though there had been in the patient an unsatisfied maternity. I am told by the highest authorities that in a certain Asiatic nation cancer of the breast is exceedingly rare. As there is a very rapid increase in the population, and a man is not confined to his wife if he can afford a concubine, there is probably no lack of the nursing satisfaction. . . . .

"Without exception, I have found the life of all cancer patients needed broadening, as plainly seen from the blow to their emotions when detached from their objective attachment."

Somehow we feel that if it were likely that this book would be taken seriously it might do a great deal of harm.

ANTIGÉNOTHÉRAPIE DE LA TUBERCULOSE. *Par les Extraits Méthyliques de Bacilles de Koch.*
By L. Nègre and A. Boquet. Preface by A. Calmette. *Masson et Cie.*
16 francs 5¼ x 7¾; 158 (paper) *Paris*

An experimental and clinical study of methyl alcohol extracts of tubercle bacilli, preliminarily treated with acetone. Such an extract, freed of its alcohol, and suspended in physiological salt solution, is found to be a potent antigen for the production of tubercular antibodies. Striking results are reported from its use in treating experimental tuberculosis in animals, and also certain forms of human tuberculosis.

ORGANISED PUBLICATION. *A Connected Series of Proposals Relating to the Publication and Record of Scientific and Technical Information.*
B. J. F. Pownall. *Elliot Stock*
5 shillings 6 x 9¾; 91 *London*

This book sets forth a carefully thought out scheme for standardization in the publication of scientific literature. Its

most important features are standardization of page size; printing journals so that they may be broken up into the equivalent of reprints; and finally a plan for standardized indexing. While there is nothing particularly novel in the separate suggestions the plan as a whole is worth the careful consideration of scientific men, in trying to solve a problem of ever-increasing difficulty.

LES CONCEPTS SCIENTIFIQUES.
By Hélène Metzger. *Félix Alcan*
12 francs *Paris*
$4\frac{5}{8}$ x $7\frac{1}{4}$; xi + 195 (paper)

This is a metaphysical discussion of the problem of classification in general. It received in 1925 the Bordin prize of the *Académie des Sciences morales et politiques*.

HISTORY OF THE SCIENCES IN GRECO-ROMAN ANTIQUITY.
By Arnold Reymond (Translated by Ruth Gheury De Bray). *E. P. Dutton and Co.*
$2.50 $4\frac{7}{8}$ x $7\frac{1}{4}$; x + 245 *New York*

An interesting, but not very important book. The best section is that on the mathematical sciences.

THE COST OF BIOLOGICAL BOOKS IN 1927

By RAYMOND PEARL

Institute for Biological Research, Johns Hopkins University

AT THE end of the first volume of the QUARTERLY REVIEW OF BIOLOGY (Vol. I, pp. 605–608, 1926) was inaugurated the plan of reporting annually on the cost of the books which had been received during the year. The present paper continues this plan with the report of book costs for the year 1927.

For the purpose of price comparison the books are classified by origin as follows:

I. *The United States.* Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of books reviewed during the year have had this origin just as in 1926.

II. *Germany.* In the number of books sent in by publishers for review Germany stands next to this country.

III. *English-American.* In this group are placed the books which are manufactured and published in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England.* In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France.* This group includes all books published in France and her colonies.

VI. *Other countries.* Here are placed all books published in any other country than those specified above.

VII. *United States Government.*

VIII. *British Government.* This is a new rubric not separately listed in the 1926 discussion. It has seemed desirable this year to make a separate item for British government publications, on the same ground that United States government publications are treated by themselves. It is unfair to include such publications with books commercially produced.

Table 1 gives, for each of these eight rubrics, (*a*) the total number of pages in the books received for review; (*b*) the total cost of these books in dollars, foreign prices being converted to dollars on the basis of the exchange prevailing when the books were received; (*c*) the average price per page *in cents*.

In order to facilitate comparison between 1926 and 1927 in respect of book prices, table 2 has been prepared. In this table the following items are included: (*a*) the average price per page, in cents, for the year 1926; (*b*) the average price per page, in cents, for the year 1927; (*c*) the absolute change in average price per page, in cents, between 1926 and 1927, a + sign denoting an *increase* in 1927 as compared with 1926, and a − sign denoting a *decrease;* (*d*) the percentage difference of the 1927 average price per page from that of 1926 taken as a base, the + sign again indicating that the

books were on the average higher in price in 1927 than they were in 1926, and the − sign that they were lower.

The data presented in tables 1 and 2 permit some interesting deductions. In the first place it is evident that a larger number of books were noticed in the QUARTERLY REVIEW OF BIOLOGY in 1927 than in 1926. The total number of pages in the books reviewed in 1926 was 82,575, while in 1927 it was 102,109, an increase of 23.7 per cent.

TABLE 1

Prices of biological books, 1927

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
English-American	9,013	$125.05	1.39
Germany	18,528	221.70	1.20
England	7,639	87.10	1.14
United States	47,779	522.40	1.09
British Government	2,520	24.18	0.96
Other countries	3,429	26.71	0.78
France	10,805	38.59	0.36
U. S. Government	2,396	5.65	0.24

TABLE 2

Comparison of the prices of biological books in 1926 and 1927

ORIGIN	AVERAGE PRICE PER PAGE 1926	AVERAGE PRICE PER PAGE 1927	ABSOLUTE CHANGE + OR −	RELATIVE CHANGE + OR −
	cents	*cents*	*cents*	*per cent*
English-American	1.55	1.39	−0.16	−10.3
Other countries	1.51	0.78	−0.73	−48.3
England	1.28	1.14	−0.14	−10.9
United States	1.12	1.09	−0.03	−2.7
Germany	1.09	1.20	+0.11	+10.0
France	0.35	0.36	+0.01	+2.9
U. S. Government	0.31	0.24	−0.07	−22.6

In 1927 as in 1926 the most expensive books were the English-American on the basis of the average price per page. But, as was pointed out last year, it must be remembered that these books had paid duty. France, this year as last, occupies the lowest position in the list for commercially published books. Its average price per page is lower than that for any other group except the United States government publications.

The most striking change in the 1927 table as compared with that for 1926 is the altered position of Germany. In last year's article the following comment was made:

"There is a widely prevailing impression that the German publishers are greatly over-pricing their products at the present time. This does not seem to be the case, so far as the present sample of new biological books is concerned. Making due allowance for the fact that the majority of the German prices included in the table are for books in paper covers, it turns out that the biological books received from Germany during 1926 cost almost exactly the same per page as those turned out by American publishers."

Table 1 of the present paper indicates that the situation has altered, so far as may be judged from the samples of German books received in 1926 and 1927. This year the German books received, which do not pay duty, had an average price per page second in the list; higher than the price of English books in England, and notably higher than American books published and sold in this country. It would be easy to suggest that the difference between the 1926 and the 1927 average is due to the QUARTERLY REVIEW OF BIOLOGY having received in 1927 an intrinsically different and more expensive class of German books in 1927 than in 1926. But a detailed examination of the books themselves does not support such an explanation. On the whole the books of the two years seem to be equivalent random samples of German scientific books

generally. We shall await with great interest the comparative showing of German biological book prices in 1928.

Table 2 exhibits the gratifying result that, with the exception of those produced in Germany, the biological books comprised in these two samples either remained at the same level of average price per page in 1927 that they held in 1926, or else declined in average price. English and English-American biological books *fell off* in price, so far as may be judged from these samples, by approximately 10 per cent. American and French average prices maintained in 1927 their 1926 level, the changes, down and up respectively, being obviously insignificant, considering the chance errors involved in the sampling. The average price per page of the German biological books here under discussion *increased* 10 per cent in 1927 over 1926. The large percentage decrease in average price of the "other countries" books shown in table 2 probably does not mean much. The samples were small in both years, and the books showed great variation in character and price. It is interesting and pleasing to note that the United States government publications showed a decrease of 22 per cent in average price per page in 1927 as compared with 1926. Is this to be regarded as one result of the "economy program" of the present administration?

If all the books noticed in the QUARTERLY REVIEW OF BIOLOGY in 1926, regardless of origin, are lumped together and compared with all the books noticed in 1927 it works out that the average price per page in 1926 was 1.097 cents, and 1.030 cents in 1927. This indicates a *decrease* in average price per page of just over 6 per cent.

In concluding these notes for the present year I should like to emphasize that the statistical nature of the basic data is such as not to permit wide generalization. We are dealing here only with very small samples of books in general, and with by no means all of the strictly biological books. Indeed for some of the countries our samples are only small fractions of the biological works there published. So the reader must be cautious in the kind of conclusions he draws from these annual reviews of the experience of the QUARTERLY REVIEW OF BIOLOGY regarding book prices.

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